
A REVISED TREATMENT OF BORAGINACEAE FOR PANAMA¹

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ABSTRACT

The Boraginaceae known from Panama now number 52 species compared with the 33 that were recognized the last time the family was treated. Eight of these are described as new species, five in the genus Cordia and three in Tournefortia. Among the new records for Panama is Moritzia lindenii, the genus being previously unknown in the country. Most genera of Panamanian Boraginaceae are South American in origin. More than half of the species are widespread in the Neotropics, but the remainder show stronger affinities with the rest of Central America than with South America or with the West Indies.

The Panamanian species of Boraginaceae have been treated numerous times since the turn of the century. Standley's floras of the Canal Zone (1928) and Barro Colorado Island (1933) predate Ivan Johnston's studies of the family, and many of the names Standley used were later placed in synonymy by Johnston, who published extensively on the family from the 1920s to the 1950s. Johnston's book *The Botany of San José Island* (1949b) treated another island flora, but unfortunately all of the works up to this time essentially describe the flora of the Canal Area. Thomas B. Croat's *Flora of Barro Colorado Island* (1978) provides an excellent treatment of the species on the island.

The Boraginaceae of Panama were treated for the entire country by Nowicke (1969) in the *Flora of Panama*. Subsequently, the number of collections from Panama increased, especially from regions then poorly known. Floristic studies in other Central

American countries have altered taxonomic concepts of some Panamanian species. Examination of collections while preparing a revision of *Cordia* for Mexico and Central America (Miller, 1985) and of floristic treatments for Nicaragua (Miller, in press) and Mesoamerica (Miller, in prep.) revealed nine previously unrecorded species as well as eight undescribed species for Panama, a significant increase from 33 to 52 species.

Five subfamilies are currently recognized within the Boraginaceae (Johnston, 1951; Cronquist, 1981): Cordioideae, Ehretioideae, Heliotropioideae, and Boraginoideae, all of which have representatives in Panama, and the Wellstedioideae, which consists of two African species. The Cordioideae and Ehretioideae have sometimes been treated together as a separate family, Ehretiaceae (Lindley, 1830; Airy Shaw, 1973; Hutchinson, 1973). They are, however, clearly related to the other three subfamilies and are tied to them by

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intermediate genera. Recent authors (e.g., Cronquist, 1981) have generally accepted their inclusion in a broadly defined Boraginaceae. Recognition of one family with five subfamilies also provides more information about relationships.

PHYTOGEOGRAPHIC RELATIONSHIPS OF PANAMANIAN BORAGINACEAE

The Boraginaceae of Panama make up an assemblage of species derived from different regions. In order to assess their phyto-geographic relationships, the distributions of the constituent genera and species were determined. The genera *Borago* and *Cynoglossum* were excluded from the generic analysis, as both are not indigenous. The remaining seven genera are listed in Table 1 with their presumed centers of origin.

Four of the seven genera are clearly South American in origin. All three species of *Moritzia* occur in South America, with only one ranging north as far as Costa Rica. Although *Cordia*, *Heliotropium*, and *Tournefortia* are pantropical in distribution, they are strongly centered in South America.

Bourreria and *Hackelia* clearly originated in North America. The majority of the species of *Bourreria* occur in Mexico, with an additional group centered in the Greater Antilles; only a few species range south to southern Central America and South America. *Hackelia* is distributed widely in north temperate regions with the greatest concentration of species in the western United States (Gentry & Carr, 1976).

Ehretia is more problematic but certainly seems to be of Old World origin. Most of its species occur in Africa but it is well represented in tropical and subtropical Asia. Whether or not this strong African representation indicates that *Ehretia* originated there or radiated there as the climate became drier at the end of the Oligocene (Raven & Axelrod, 1974) is not clear. Regardless, *Ehretia* is poorly represented in the New World, with only three species, and the southern limit of distribution is in Chiriquí Province of western

Panama. The presence of *Ehretia* in Panama, then, probably results from southward migration.

From this it seems clear that the generic affinities of Panamanian Boraginaceae are predominantly South American. Four of the seven genera that account for all but four of the native Panamanian Boraginaceae are centered in South America. *Hackelia* and *Bourreria* are North American in origin and, at least in the New World, so is *Ehretia*. The strong South American tie agrees with other analyses at familial or generic levels. Gentry (1985) reported that 84% of the plant species in Panama were members of Gondwanaland families, and Karr (1985) reported that at least 50% of the bird species in Panama were members of families that were South American in origin.

Distributions of Panamanian species of Boraginaceae are summarized in Table 2 following Davidse's (1985) format. Distributional data were derived from herbarium specimens and literature (Gentry & Carr, 1976; Gibson, 1970; Johnston, 1924, 1927, 1928, 1930, 1935, 1940, 1949a, c, 1950; Miller, 1985, in press; Nash & Moreno, 1981; Nowicke, 1969). Each species was scored for presence in North America, Central America, South America, and the West Indies. In addition, presence in the Old World or cultivated status was noted.

INTRODUCED SPECIES

Two introduced species of Boraginaceae are known from Panama. *Borago officinalis* L. is widely cultivated throughout the world and occasionally is found naturalized, although these populations do not appear to persist for long. *Cynoglossum amabile* Stapf & J. R. Drumm. is a native of China originally imported as an ornamental and has become established in numerous localities at high elevations in the Neotropics.

COSMOPOLITAN SPECIES

Two species, *Heliotropium curassavicum* L. and *H. indicum* L., are widespread in the

TABLE 1. *Native genera of Panamanian Boraginaceae and presumed centers of origin.*

Genus (Number of Species)	Number of Species in Panama	% of Pana- manian Species	Center of Origin
<i>Bourreria</i> (50)	2	4	North America
<i>Cordia</i> (300+)	27	54	South America
<i>Ehretia</i> (50)	1	2	Paleotropics
<i>Hackelia</i> (45)	1	2	North America
<i>Heliotropium</i> (150)	4	8	South America
<i>Moritzia</i> (3)	1	2	South America
<i>Tournefortia</i> (150)	14	28	South America

New World and have become widespread in the Old World as introduced weeds (Nowicke & Miller, in press).

NORTHERN SPECIES

Seven species of borages reach their southern limits in Panama. A single species each of *Bourreria* and *Ehretia*, both genera probably northern in origin, are included in this group. Five Central American species of *Cordia* make up the remainder of this group, of which four are Central American species of lowland wet forests. *Cordia diversifolia* Pa-

vón ex A. DC. and *C. megalantha* S. F. Blake range north to Veracruz in southern Mexico; *C. lucidula* I. M. Johnston and *C. porcata* Nowicke range only as far north as Nicaragua. These four belong to Central American species groups. The fifth, *Cordia inermis* (Miller) I. M. Johnston, reaches from Panama north to Sinaloa, Mexico in dry disturbed areas. It is a member of a group of about eight species that is widespread in the Neotropics of which *Cordia foliosa* Martens & Galeotti is the only other species restricted to Central America.

NORTHERN-SOUTHERN SPECIES

Twenty-seven species, comprising slightly more than half of the Boraginaceae known from Panama, range widely in the Neotropics. With two exceptions, all of these are truly widespread species that indicate no particular geographic affinity. The genus *Moritzia* consists of three species and is entirely restricted to South America except for *M. lindonii* (A. DC.) Gürke ex Benth., which ranges north to Costa Rica. *Hackelia* is a northern genus, but *H. mexicana* (Schldl. & Cham.) I. M. Johnston is widespread in Central America

TABLE 2. *Distributions of Panamanian Boraginaceae.*

Category ¹	Number of Species	Combined Categories	Number of Species	% of Flora
1. Cultivated	1	Introduced	2	4
2. Alien Weeds	1			
3. Cosmopolitan ²	2	Cosmopolitan	2	4
4. CA & WI & NA	0	Northern	7	13
5. CA & WI	0			
6. CA & NA	0			
7. WI & NA	0			
8. CA	7	Southern	0	0
9. SA & WI	0			
10. SA	0	Southern-Northern Combination	27	52
11. CA & SA & WI & NA	3			
12. CA & SA & WI	11			
13. CA & SA & NA	0			
14. CA & SA	13	Endemic Element	14	27
15. Panama	7			
16. Panama & Costa Rica	4			
17. Panama & Colombia	3			

¹ Abbreviations: CA = Central America (Costa Rica-Tropical Mexico); NA = North America (United States to Subtropical Mexico); SA = South America; WI = West Indies.

² Includes all native American species distributed on at least one Old World continent.

TABLE 3. *Endemic elements among the Boraginaceae of Panama and distributions.*

Species	Distribution ¹	Elevation (m)
<i>Cordia anisophylla</i>	CN, DA, PA, SB	0-1,000
<i>Cordia correae</i>	CC, PA, VE	800-1,000
<i>Cordia croatii</i>	CC, VE, Costa Rica	800-1,200
<i>Cordia lasiocalyx</i>	BT, CA, CC, DA, PA	0-800
<i>Cordia leslieae</i>	PA	800-1,000
<i>Cordia protracta</i>	SB, Colombia	sea level
<i>Cordia tacarcunensis</i>	DA, Colombia	100
<i>Tournefortia brenesii</i>	VE, Costa Rica	800-1,350
<i>Tournefortia johnstonii</i>	CH, VE, Costa Rica	1,000-1,300
<i>Tournefortia longispica</i>	BT, CH, CC, VE	600-1,500
<i>Tournefortia multiflora</i>	CN, VE	400-900
<i>Tournefortia ramonensis</i>	BT, CH, Costa Rica	2,000-3,000
<i>Tournefortia tacarcunensis</i>	DA, Colombia	1,500
<i>Tournefortia urceolata</i>	CH, CN, SB	400-2,300

¹ Abbreviations for provinces: BT = Bocas del Toro; CA = Canal Area; CH = Chiriquí; CC = Coclé; CN = Colón; DA = Darién; PA = Panamá; SB = San Blas; VE = Veraguas.

and the Andes. *Cordia* and *Tournefortia* contain 22 of the widespread species, all of which are found in most of Central America, but only about one-third of them range as far south as southern Brazil and Argentina. The majority have southern limits of distribution in northern South America or extend south only in the Andes.

ENDEMICIS

Fourteen species of Panamanian borages, all species of *Cordia* and *Tournefortia*, are known only from Panama and adjacent Colombia or Costa Rica. Seven are known only from Panama (Table 3); three range slightly into Colombia, and four others extend into Costa Rica. All are relatively rarely collected. Eight are described as new in this paper. All of the species of *Tournefortia* and three of *Cordia* occur at mid to high elevations, while the widespread taxa generally inhabit lowlands.

More than half of the Panamanian species of Boraginaceae are widespread or introduced and are not helpful in indicating geographic affinity. The pattern of the lowland Panamanian flora being composed primarily of South American elements has been reported for other groups (Davidse, 1985; Raven & Axelrod, 1974, 1975). Hammel (1986) found a similar pattern for a subset of the flora of

La Selva in lowland Costa Rica. The fourteen endemic elements indicate that the Panamanian flora is old enough to have become distinct from that of surrounding areas. The relationships of the endemics are poorly understood but the majority are probably with species of Colombia and Ecuador. Seven species have distributions extending to the north, and many are members of species complexes restricted to Mexico and Central America. These species, and the absence of southern elements, indicate that Panamanian borages have a stronger relationship at the species level with Central America than with South America. Although most of the species belong to originally South American genera, a significant portion of these seem to have reached Panama from the north, perhaps as a result of secondary radiations of *Cordia* and *Tournefortia* in Mexico and northern Central America.

SYSTEMATIC TREATMENT

Boraginaceae Juss., Gen. Pl. 128. 1789.

Trees, shrubs, lianas, vines, or herbs, often conspicuously pubescent, the hairs often with a basal cystolith. Leaves estipulate, simple, alternate or rarely opposite. Inflorescence cymose to paniculate, the branches often scorpioid, helicoid, or reduced and capitate to

glomerate. Flowers perfect or imperfect, usually 5-merous; calyx usually persistent, tubular to campanulate, usually 5-lobed; corolla gamopetalous, usually 5-lobed; stamens usually as many as the corolla lobes and alternate with them; ovary superior, 2-carpellate but often becoming falsely 4-locular; ovules usually 4, anatropous; style 1, terminal or gynobasic, simple or branched; stigmas 1–4. Fruits drupaceous and 1–4-seeded, sometimes dry at maturity, or of 4 nutlets.

The Boraginaceae are worldwide in distribution and comprise about 100 genera with approximately 2,000 species. Nine genera are known from Panama containing 52 species. Although no collections of the genus *Borago* are known from Panama, the European species *Borago officinalis* L. is often cultivated in gardens in other parts of Tropical America and is included here as it undoubtedly occurs in Panama.

KEY TO THE GENERA OF BORAGINACEAE IN PANAMA

- 1a. Plants trees or shrubs; stigmas 2 or 4; fruits fleshy at least when young.
 2a. Style twice divided into 4 stigmas *Cordia*
 2b. Style once divided into 2 stigmas.
 3a. Calyx lobes valvate; corolla fleshy, longer than 8 mm *Bourreria*
 3b. Calyx lobes imbricate or open in bud; corolla thin, shorter than 5 mm *Ehretia*
- 1b. Plants herbs, lianas, vines, or clambering shrubs, rarely small trees; stigma 1; fruits dry except in *Tournefortia*.
 4a. Fruits entire to shallowly 4-lobed; style terminal; corolla white, green, or yellow-green, rarely purple.
 5a. Plants woody; fruits fleshy *Tournefortia*
 5b. Plants herbaceous; fruits dry *Heliotropium*
- 4b. Fruits deeply 4-lobed, consisting of 4 separate nutlets or the nutlets solitary by abortion in *Moritzia*; style gynobasic; corolla blue.
 6a. Calyx campanulate to rotate.
 7a. Nutlets with glochidiate spines; calyx lobes less than 4 mm long.
 8a. Cauline leaves clasping at base; nutlets spreading, the spines ca. 0.5 mm long *Cynoglossum*
 8b. Cauline leaves cuneate to decurrent but not clasping at base; nutlets erect, the spines 1–4 mm long *Hackelia*
 7b. Nutlets lacking spines, shallowly ribbed; calyx lobes more than 10 mm long *Borago*
 6b. Calyx cylindrical *Moritzia*

Borago L., Sp. Pl. 137. 1753; Gen. Pl. ed. 5. 67. 1754. TYPE: *Borago officinalis* L., Sp. Pl. 137. 1753.

Annual or perennial herbs, the stems hirsute. Leaves alternate, the basal ones petiolate, the cauline ones sessile. Inflorescence a corymbose group of racemes, bracteate. Flowers bisexual; calyx with 5 lobes, these free to nearly the base; corolla broadly campanulate to rotate, the 5 lobes imbricate, the tube short, appendaged in the throat; stamens 5, exserted, the filaments broad, the anthers linear; ovary 4-lobed, the ovules 4, the style gynobasic, filiform, the stigma emarginate. Nutlets 4, obovoid or oblong, the gynobase flat or nearly so.

Borago comprises three species from southern Europe and the Mediterranean re-

gion, one of which, *Borago officinalis*, is widely cultivated.

Borago officinalis L., Sp. Pl. 137. 1753.

TYPE: without locality or collector (holotype, LINN (Savage Catalog number 188.1), not seen; microfiche, MO).

Annual herb, 30–60 cm tall, the stems coarsely hirsute. Basal leaves petiolate, ovate to oblong, 6–12 cm long, 2–6 cm wide, the apex acute to obtuse, the base cuneate and decurrent along the petiole, the margin entire to irregularly undulate, the adaxial surface hirsute to scabrous, the veins prominent, the lower surface pubescent with most of the hairs restricted to the veins, the uppermost leaves sessile, lanceolate. Inflorescence loosely racemose, bracteate, the rachis hirsute. Flowers borne on pedicels 1–5 cm long; calyx rotate, with 5 lanceolate lobes to 10–18 mm

long, 2–3 mm wide, hirsute; corolla blue, yellow in the throat, rotate, 18–22 mm long, the 5 lobes ovate to lanceolate, 8–11 mm long, the tube to 3 mm long; stamens 5, the filaments to 2 mm long, broad, the anthers lanceoloid, 5–7 mm long, with an appendage to 3 mm long at the base; ovary ca. 2 mm broad, the 4 lobes globose, the style 5.5–7.5 mm long. Fruits with the calyx and style persistent, the 4 nutlets obovoid, 4–6 mm long, 2–3 mm broad, finely ribbed, tuberculate at the apex.

Distribution. *Borago officinalis* is native in Europe, north Africa, and adjacent Asia but is widely cultivated and occasionally becomes naturalized.

Although *Borago officinalis* has not been collected in Panama, it seems almost certain that it is present in Panamanian gardens. It is often cultivated as a culinary or medicinal herb and is known from most neotropical countries, often as an adventive.

Bourreria P. Browne, Civ. Nat. Hist. Jamaica. 168. 1756; nom. cons. TYPE: *Bourreria succulenta* Jacq., Enum. Syst. Pl. 14. 1760; Select. Stirp. Amer. Hist. 44. 1763.

Trees or shrubs. Leaves alternate, petiole late, the margin usually entire. Inflorescences terminal cymes. Flowers bisexual, actinomorphic; calyx campanulate, 2–5-merous, the lobes valvate in bud; corolla relatively large, salverform, white to yellow in the Central American species, usually 5-merous, the lobes imbricate in bud; stamens 5, the filaments adnate to the base of the tube, the anthers ovate to oblong; ovary 4-locular, the style terminal, bifid; stigmas 2, flattened. Fruits drupaceous, enclosing 4 bony nutlets, the endosperm carnosous, the cotyledons flat.

Bourreria has been considered to comprise about 50 species (Airy Shaw, 1973); however, Gibson's (1970) estimate of 15–20 species is probably more realistic. This poorly understood genus needs revision. Numerous species have been published based upon minor variations in leaf shape and indument—res-

olution of the problems this has created will necessitate field study of these characters. *Bourreria* ranges from Mexico and southern Florida through the West Indies and Central America to northern South America, with the majority of the species occurring in Mexico and the West Indies. About seven species are known from Central America, although only two have been found in Panama. Despite considerable confusion about delimitation of species, the two known from Panama are among the most distinct and easily recognized members of the genus.

De Candolle (1845) placed the species currently recognized as belonging to *Bourreria* in *Ehretia* sect. *Bourreria* (P. Browne) DC. All recent authors have, however, accepted *Bourreria* as distinct generically on the basis of its valvate calyx lobes and corollas that are larger and more fleshy than those in *Ehretia*. Miers (1869) pointed out that *Bourreria* has fruits that dry at maturity and separate into four single-seeded pyrenes with an apical attachment, whereas species of *Ehretia* have drupaceous fruits that usually remain entire at maturity, probably until they are dispersed. They later divide into two 2-seeded pyrenes.

KEY TO THE SPECIES OF *BOURRERIA* IN PANAMA

- 1a. Corollas 28–48 mm long; most leaf blades greater than 12 cm long *B. costaricensis*
- 1b. Corollas 8–12 mm long; most leaf blades less than 12 cm long *B. oxyphylla*

Bourreria costaricensis (Standley) A. Gentry, Phytologia 26: 67. 1973. *Schlegelia costaricensis* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1128. 1938. TYPE: Costa Rica. Alajuela: cataratas de San Ramón, Mar. 1931, A. M. Brenes 13570 (holotype, F 857116; isotype, NY).

Bourreria superba var. *glabra* Schery, Ann. Missouri Bot. Gard. 29: 366. 1942. *Bourreria panamensis* I. M. Johnston, J. Arnold Arbor. 29: 229. 1948. TYPE: Panama. Bocas del Toro: Chiriquí Lagoon, Isla Colón, 3 June 1941, H. von Wedel 2472 (holotype, MO, not seen).

Tree 10–15 m tall, the twigs glabrous. Leaves persistent; petioles 10–25 mm long, glabrous; leaf blade elliptic to obovate, 6.5–

23.5 cm long, 3.7–10.5 cm wide, the apex obtuse to rounded and sometimes mucronate, the base acute to cuneate, the margin entire, the adaxial and abaxial surfaces glabrous. Inflorescence a small terminal cyme. Flowers sessile, bisexual; calyx campanulate, 13–18 mm long, 10–18 mm wide at the mouth, glabrous, the 5 lobes triangular; corolla white, broadly funnelform, 2.8–4.8 cm long, 5-merous, the lobes depressed ovate; stamens 5, the filaments 18–20 mm long, the upper 14–18 mm free, slightly puberulent at the point of insertion, the anthers narrowly ellipsoid, 4 mm long. Fruits green, globose, 2–2.5 cm diam.

Distribution. This species occurs in wet to moist forests from sea level to 1,700 m from Nicaragua to Panama. In Panama it is known from Bocas del Toro and Colón.

This is one of the most distinctive species of *Bourreria* with its large, funnelform corollas more than 2.5 cm long. It is quite similar to *Bourreria superba* I. M. Johnston of western Mexico in general appearance but is widely separated geographically and grows in a very different habitat. *Bourreria costaricensis* differs further from *B. superba* by having glabrous twigs, leaves, and staminal filaments.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Chiriquí Lagoon, Isla Colón, *Wedel 2974* (MO). CHIRIQUÍ: Fortuna Dam area, 1,200 m, *McPherson 6782* (MO); Fortuna Dam Region, near forestry experimental station, S of lake, 1,150 m, *McPherson 7873* (MO). COLÓN: Santa Rita Ridge Road, near junction of Trans-isthmian Highway, *D'Arcy et al. 15554* (MO).

Bourreria oxyphylla Standley, *Trop. Woods* 16: 40. 1928. TYPE: Belize. El Cayo: San José, Nov. 1927, *J. B. Aitken 4* (holotype, F 572622).

Beureria wagneri Standley in Yuncker, *Publ. Field Mus. Nat. Hist., Bot. Ser.* 9: 328. 1940. TYPE: Honduras. Atlántida: foothills back of La Ceiba, 23 July 1938, *T. G. Yuncker, J. M. Koepfer & K. A. Wagner 8608* (holotype, F 941533).

Shrub or small tree to 5(–15) m tall, and ca. 1 m diam., the twigs glabrous to puber-

ulent or sparsely strigillose. Leaves persistent, the petioles 7–17 mm long, glabrous to puberulent, the blades elliptic to elliptic-oblong, 4.5–10.5 cm long, 2–5 cm wide, the apex acute to obtuse and often abruptly short acuminate, the base acute to obtuse, the margin entire, the adaxial surface glabrous, the abaxial surface essentially glabrous but sparsely puberulent along the major veins. Inflorescence terminal, cymose, to 9 cm broad, the branches sparsely to evenly strigillose to puberulent. Flowers sessile, bisexual; calyx narrowly campanulate, 5–6 mm long, strigillose to puberulent, the 3–5 lobes deltate and often bifid at the apex; corolla white to pale green, tubular with spreading lobes, 8–12 mm long, 5-merous, the lobes oblong-obovate, 5–6 mm long, the tube 5–6 mm long; stamens 5, exserted, the filaments 3–4 mm long, glabrous, the anthers oblong, 2–3 mm long; ovary ovoid, 1.5–2 mm long, the disc annular, the style 6–8 mm long, the stigmas discoid. Fruits yellow to orange and later turning black, ovoid to subglobose, 6–12 mm long, 5–11 mm broad.

Distribution. *Bourreria oxyphylla* is known from southern Mexico through Belize to Nicaragua with a single collection from San Blas in Panama and a few collections from Colombia. It occurs in wet forests, where it ranges from sea level to nearly 800 m in elevation.

Bourreria oxyphylla is distinctive and is one of only two members of the genus in Central America with glabrous, elliptic leaves; the other, *Bourreria costaricensis*, is readily separated by its larger leaves, some to 10.5 cm wide, and corollas more than 2.8 cm long. *Bourreria wagneri* was described from a population in Honduras with slightly more puberulent twigs but is otherwise identical to other populations and is not recognized as distinct. The southern populations from Panama and Colombia have slightly larger, less lustrous leaves than the populations from northern Central America, but the differences

are slight and they do not seem to warrant taxonomic recognition.

Additional specimens examined. PANAMA. SAN BLAS: island of Soskatupu, west end, *Kirkbride 195* (MO).

Cordia L., Sp. Pl. 190. 1753; Gen. Pl. ed. 5. 87. 1754. TYPE: *Cordia sebestena* L., Sp. Pl. 190. 1753.

Trees or shrubs. Leaves alternate, deciduous or persistent, petiolate, the petioles usually adaxially canaliculate. Inflorescence cymose, paniculate, spicate, capitate, or glomerate. Flowers perfect, or unisexual by abortion, with the plants then dioecious; calyx 3-5(-10)-lobed or rarely circumscissile; corolla funnelform, campanulate, or tubular with reflexed or spreading lobes, (4-)5(-18)-lobed, or sometimes the lobes nearly lacking and the corolla apically undulate to frilled or nearly truncate; stamens as many as corolla lobes, the lower part of the filaments adnate to corolla tube, often with hairs at or near insertion, the anthers oblong to ellipsoid; ovary entire, falsely 4-locular; disc annular to crateriform; style terminal, twice bifid, the 4 stigma lobes clavate, filiform, or discoid. Fruits borne with the calyx persistent, variable, dry with a fibrous wall and capped by the persistent, cartilaginous base of the style (sect. *Gerascanthus*), dry and bony-walled (sect. *Rhabdocalyx*), or with a thin exocarp, juicy to mucilaginous mesocarp, and bony endocarp (sects. *Varronia*, *Myxa*, and *Cordia*), usually

1-locular and 1-seeded, the endosperm lacking, the cotyledons plicate.

The pantropical genus *Cordia* is the largest in the family: there are about 300 species, mostly neotropical. Species of *Cordia* are found in a wide variety of habitats, but, although many species can be found in wet forests, those found in dry, disturbed areas are a more important component of the vegetation.

Cordia is the only Panamanian genus of the Cordioideae. The South American genera, *Auxemma* Miers and *Patagonula* L., differ from *Cordia* in the unusual form of their fruiting calyces and by having short styles and monomorphic flowers. Although clearly related to *Cordia*, they seem to represent a distinct lineage. *Cordia*, however, is a very diverse assemblage, and a number of authors have suggested dividing it into 3-12 segregate genera (Mez, 1890; Friesen, 1933; Nowicke & Ridgway, 1973). Nevertheless, *Cordia* sensu lato appears to be a distinct monophyletic group and its division into narrowly defined genera seems unwarranted. Johnston (1930, 1940, 1949a, b, 1950, 1951) treated the genus in a broad sense and recognized five to seven sections in his various works. Recent authors (Nowicke, 1969; Gibson, 1970; Nowicke & Ridgway, 1973; Opler et al., 1975; Miller, 1985) have recognized five sections. Twenty-seven species in four of the sections are known from Panama.

KEY TO THE SPECIES OF *CORDIA* IN PANAMA

- 1a. Corolla bright red-orange; fruit drupaceous and totally enclosed in the accrescent calyx at maturity (sect. *Cordia*) *C. sebestena*
- 1b. Corolla white to yellow; fruit not totally enclosed by the calyx at maturity or if enclosed, then not drupaceous.
 - 2a. Corolla marcescent; fruit with a fibrous wall (sect. *Gerascanthus*).
 - 3a. Ant domatia present at the base of the inflorescences; leaves and twigs with stellate hairs; corolla lobes oblong *C. alliodora*
 - 3b. Ant domatia absent; leaves and twigs glabrous; corolla lobes deltate or ovate *C. megalantha*
 - 2b. Corolla deciduous; fruit with a bony wall.
 - 4a. Trees or shrubs with few stems; leaf margin entire or denticulate; inflorescences cymose to paniculate, branching more than twice; fruits generally asymmetrical (sect. *Myxa*).
 - 5a. Corolla yellow to almost white; calyx circumscissile and striate *C. dentata*
 - 5b. Corolla white; calyx opening with valvate lobes or if circumscissile than not striate.
 - 6a. Calyx costate; leaf margin with short, filiform teeth toward the apex or entire *C. diversifolia*

- 6b. Calyx smooth or striate, not costate; leaf margin entire.
- 7a. Ovary and fruit strigillose *C. bicolor*
- 7b. Ovary and fruit glabrous.
- 8a. Adaxial leaf surface evenly strigillose or scabrous to strigose; plants usually dioecious.
- 9a. Corolla tube 1.5–3.9 mm long; fruits ovoid, 6–10 mm long.
- 10a. Stems and peduncles with simple hairs; the larger leaves generally 6.5–13.5 cm wide *C. panamensis*
- 10b. Stems and peduncles with echinate hairs; the larger leaves generally 11.2–20.4 cm wide *C. cymosa*
- 9b. Corolla tube ca. 10–12 mm long; fruits ellipsoid, 8.5–16.5 mm long *C. anisophylla*
- 8b. Adaxial leaf surface glabrous or nearly so; plants usually with bisexual flowers, these usually distylous, dioecious only in *C. collococca* and *C. tacarcunensis*.
- 11a. Leaf margin distinctly revolute.
- 12a. Stems sub-alate; abaxial leaf surface glabrous; leaves not bullate *C. leslieae*
- 12b. Stems not winged or ridged; abaxial leaf surface velutinous; leaves bullate *C. dwyeri*
- 11b. Leaf margin not or only slightly revolute.
- 13a. Corolla campanulate *C. eriostigma*
- 13b. Corolla tubular, with reflexed or spreading lobes.
- 14a. Calyx distinctly 5-lobed.
- 15a. Inflorescences axillary, numerous on a single stem; plants dioecious *C. tacarcunensis*
- 15b. Inflorescences terminal or subterminal, few per stem; plants with bisexual flowers.
- 16a. Fruits white; leaf blades falcate *C. protracta*
- 16b. Fruits red or orange; leaf blades flat, not falcate *C. correae*
- 14b. Calyx (2–)3(–4)-lobed, circumscissile or dehiscing irregularly.
- 17a. Plants hermaphroditic; leaves persistent; flowers borne on current season's growth.
- 18a. Apex of the leaf caudate, the caudex 1–3.5 cm long *C. lasiocalyx*
- 18b. Apex of the leaf acuminate.
- 19a. Leaf blade elliptic to elliptic-ovate, less than 5 cm wide, usually less than 8 cm long *C. croatii*
- 19b. Leaf blade ovate to narrowly elliptic or lance-elliptic, usually more than 5 cm wide, usually more than 8 cm long.
- 20a. Fruit red, the stone not rostrate; anthers 1.1–1.2 mm long; calyx 3–4 mm long *C. lucidula*
- 20b. Fruit white, the stone not rostrate; anthers 1.9–2.3 mm long; calyx 5.2–6.5 mm long *C. porcata*
- 17b. Plants dioecious; leaves deciduous; flowers usually borne below the current season's growth *C. collococca*
- 4b. Shrubs, usually multistemmed; leaf margin serrate to minutely denticulate; inflorescences condensed, spicate, capitate, or if cymose, then less than 2.3 cm broad, dichotomous, and branching only twice; fruits symmetrical or nearly so (sect. *Varronia*).
- 21a. Inflorescences spicate.
- 22a. Leaf blade lanceolate; inflorescences terminal *C. curassavica*
- 22b. Leaf blade ovate; inflorescences axillary, the peduncle adnate to the petiole *C. spinescens*
- 21b. Inflorescences cymose or capitate.
- 23a. Inflorescence branched, cymose *C. bifurcata*
- 23b. Inflorescence capitate.
- 24a. Calyx lobes with prolonged filiform tips.
- 25a. Peduncles 0.5–2 cm long; corolla 5–10 mm long *C. globosa*
- 25b. Peduncles 3–7 cm long; corolla 3–6 mm long *C. bullata*
- 24b. Calyx lobes acute to acuminate but lacking prolonged tips.
- 26a. Inflorescences terminal or internodal *C. inermis*
- 26b. Inflorescences axillary *C. linnaei*

Cordia alliodora (Ruíz Lopez & Pavón) Oken, *Allg. Naturgesch.* 2(2): 1098. 1841. *Cerdana alliodora* Ruíz Lopez & Pavón, *Fl. Peruv.* 2: 47, pl. 184. 1799. TYPE: Peru. Huanuco: Pozuzo, *Hipólito Ruíz & José Pavón* (holotype, B, not seen; photo, MO).

Tree to 20(-25) m tall, the twigs stellate-pubescent when young, ending in obovoid ant domatia. Leaves deciduous; petioles (5-)8-28(-35) mm long, stellate-pubescent; blade elliptic to narrowly elliptic or slightly obovate, (3.5-)5-17(-20.5) cm long, (1.4-)2-7(-8.5) cm wide, the apex acuminate or acute, the base acute to obtuse, the adaxial surface glabrous to sparsely stellate-pubescent, the abaxial surface sparsely to densely stellate-pubescent. Inflorescence terminal, usually arising from an obovoid ant domatium, paniculate, to 25(-30) cm broad, the branches usually densely stellate-pubescent. Flowers borne on short spurs to 1.5 mm long, bisexual, monomorphic; calyx tubular, (4-)4.5-5.5(-6.5) mm long, 10(-12)-ribbed, stellate-pubescent, with (4-)5(-6) small teeth; corolla marcescent, white, (8.5-)9.5-12(-14) mm long, (4-)5(-6)-merous, the lobes oblong, (4.5-)5-7(-8.5) mm long, the tube (3.5-)4.5-6(-8.5) mm long; stamens (4-)5(-6), the filaments 9-12 mm long, the upper (3.5-)5.5-7.5 (-9) mm free, sparsely pubescent at insertion, the anthers oblong, 1.5-2(-2.5) mm long, borne at the same height or above the stigmas; ovary ovoid to very broadly ovoid, (0.7-)1-2(-2.5) mm long; disc depressed obovoid to very broadly obovoid, 0.5-1 mm tall; style 4.5-6.5 mm long, the stigma lobes clavate. Fruits enclosed by the persistent corolla and calyx, ellipsoid, (4.5-)5-7(-8) mm long, (1-) 2-2.5 mm broad, the wall thin, fibrous.

Distribution. *Cordia alliodora* occurs in dry to wet forests from sea level to 1,100 m in elevation and ranges from Mexico to South America and to the West Indies. This species is known from all provinces in Panama.

Cordia alliodora is the widest-ranging species of the genus. Its ant domatia and

stellate indument are distinctive. It is also one of only two homostylous species in sect. *Gerascanthus*, the other being *Cordia trichotoma* (Vell.) Arráb. ex Steudel of southern South America (Gibbs & Taroda, 1983). This condition is derived in the section, and these two species form a monophyletic group further characterized by stellate hairs on the stems and leaves and by flowers considerably smaller than those of their relatives. The flowers of *Cordia alliodora* vary from short-style to forms with the stigmas and anthers borne at about the same height, but individual plants appear to be constant in the ratio of anther and stigma height. No plants have been found with styles exceeding the stamens considerably.

Cordia alliodora is valued as a timber tree and, for this reason, there has been a great deal of interest recently in establishing plantations of it throughout Central America (Stead, 1980). Flowering occurs at the onset of the dry season with fruits maturing and being dispersed during mid dry season. Common names include Laurel, Laurel Blanco, and Laurel Negro.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Almirante region, *Cooper & Slater* 22 (CFMR, F, US); Changuinola Valley, *Dunlap* 291 (F, GH, US); vicinity of Chiriquí Lagoon, Old Bank Island, *Wedel* 1877 (MO, US). CANAL AREA: Summit Area, *Avilla* 302 (MO); U.S. Army Tropic Test Center, Fort Clayton, vicinity Gorgas Hospital, *Blum* 2210 (MO, SCZ); between Gatún and Bohío, *Christopherson* 118 (US); Barro Colorado Island, *Croat* 4799 (F, SCZ); 7694 (MO); 8104 (F (3), MO, NY, SCZ); 8164 (MO); 8401 (F, MO); Gaillard Highway, 2 mi. NW of Summit Garden, *Croat* 14048 (MO); Barro Colorado Island, *D'Arcy* 3931 (C, MO, TEX); Albrook, U.S. Army Tropic Test Center Site, *Dwyer & Robyns* 56 (BR, MO); Barro Colorado Island, *Foster* 719 (F, MICH); Curundu, *Harvey* 5249 (F); in government forest along Las Cruces trail, 75 m, *Hunter & Allen* 449 (BR, F, G, MO, NY, P, UC, US); near Gamboa, along edge of Canal, dump 4 area, along shore side, *Kennedy & Steiner* 2453 (C, CAS, ENCB, F, L, MO, NY, US); vicinity of Culebra, *Maxon* 4901 (C, F, NY, US (2)); roadside near RR along Panama Canal, 1½ km W of Gamboa, *Nee & Mori* 3596 (CFMR, MO); near Gamboa, *Piper s.n.* (GH (2)); Chiva-Chiva Trail, *Piper* 5755 (GH, NY, US); vicinity of Ancon, *Piper* 6007 (US); Barro Colorado Island, *Shattuck* 780 (GH, MO), 789 (MO (2)); along the old Las Cruces trail, between Fort Clayton and Corozal, *Standley* 29229 (US); between France Field, Canal Zone, and Catival, province of Colón, *Standley* 30200 (US); Fort Clayton, Cardenas Creek Area, *Tyson* 3473 (MO, SCZ); vicinity of Fort Clayton,

Walker 1 (UC); Ancon, *Wheeler & Zetek s.n.* (GH (2)); Barro Colorado Island, *Wilson 80* (F, MO); *Woodworth & Vestal 590* (F, MO). CHIRIQUÍ: 1 km carretera a Los Citricos, *Barrera 46* (MO); vicinity of San Felix, 0–120 m, *Pittier 5279* (US). COCLÉ: Penonomé and vicinity, 50–1,000 ft., *Williams 326* (NY (2), US), 327 (NY). COLÓN: Juan Mina, Río Chagres, 25 m, *Allen 4198* (G, MO); entres Brazo sawmill, Icacal which is in between Salud y Boca de Río Indio, *Howell 27* (MO). DARIÉN: Battelle Memorial Institute, sea level, Canal Bioenvironmental Program, *Duke 8145* (MO); near mouth of Río Paya on Río Tuirá, *Gentry 4349* (MO); Quebrada “Cama-chimuricate” cerca casa de Bartolo, *Kennedy 2870* (MO). HERRERA: vicinity of Ocú, hill above the cantera of Sr. Joaquin Carrizo, limestone area, *Stern et al. 1721* (MICH, MO, US). LOS SANTOS: Los Toretos, *Dwyer 2430* (MO, US); vicinity of Tonosi, Guanico, 117 ft., *Stern et al. 1856* (MICH, MO, US). PANAMÁ: Río Las Lajas, 20 m, *Allen 1607* (F, MO, NY, US); Island of Taboga, *Barclay 981* (F, US); a orillas del Río Aguacate cerca de Nuevo Arraijan, *Cedeno 13* (F, MO); en El Jobo, San Carlos, *Gonzalez 19* (F, MO); Isla Taboga, *Hjerting & Rahn 617* (C, US); San José Island, *Johnston 570* (GH); near Chepo, *Kluge 3* (CFMR, US); Isla Taboga, *Macbride 2822* (F, GH, US); Chepo, *Paul 326* (US). SAN BLAS: Permé, *Cooper 649* (CFMR, DS, F, US); mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi. inland, *Lewis et al. 154* (MO). VERAGUAS: border of Veraguas, Coclé, and Herrera provinces along the Río Santa María near bridge of Panamerican Highway, 16 km SW of Aguadulce, 0–50 m, *Knapp et al. 3348* (MO).

Cordia anisophylla James S. Miller, sp. nov. TYPE: Panama. Colón: Santa Rita Ridge Road, 9 km from Boyd–Roosevelt Highway, 350 m, Premontane Wet Forest, 15 Mar. 1975, *S. Mori & J. Kalkunki 5076* (holotype, MO 2664952; isotypes, MO, US). Figure 1.

Arbor ad 8 m alta. Folia persistentia, petiolis (4–)6–12 mm longis; laminae anisophyllae, foliis maioribus ovatis ad lanceolato-ovatis, 10.5–21(–26) cm longis, (3–)5–12.5 cm latis, minoribus ovatis ad cordatis, (3.5–)7.5–8.5(–13.5) cm longis, 4.5–7.3(–14) cm latis, apice acuminatis ad acutis, basi obtusis, superficie strigillosa, pagina inferiore strigillosa ad pilosa. Inflorescentiae terminales in axillis ramorum dispositae, cymosae. Flores heterostyli; calyx tubuliformis, 7–9 mm longus; corolla alba, tubuliformis, 10–12 mm longa, 5-lobata; stamina 5, antheris oblongis. Fructus drupaceus, putamine inaequaliter ovoideo, 8.5–16.5 mm longo, 6–7.5 mm lato.

Small erect tree or large shrub to 5(–8) m tall, the bark brown, smooth, lateral branching dichotomous in a horizontal plane, the twigs strigillose to pilose. Leaves persistent; petioles (4–)6–12 mm long, canaliculate adaxially, strigillose to pilose; blades anisophyllous, the larger ones ovate to ovate-lan-

ceolate, 10.5–21(–26) cm long, (3–)5–12.5 cm wide, the smaller ones orbicular, (3.5–)7.5–8.5(–13.5) cm long, 4.5–7.3(–14) cm wide, the apex acuminate, the base subobtusely to obtuse, the margin entire, the adaxial surface evenly strigillose, the abaxial surface strigillose to unevenly pilose. Inflorescences terminal or borne in the axils of branches, rarely internodal, loosely branched cymes, the peduncle 5–10(–13.5) cm long, strigillose to nearly pilose. Flowers sessile, distylous; calyx tubular, 7–9 mm long, 3 mm wide at mouth, the 5 lobes ± deltate, 1.8 mm long, ribs absent, strigillose, densely pilose on interior surface; corolla white, tubular with reflexed lobes, ca. 10–12 mm long, 5-merous, the lobes 2.7 mm long, 1.8 mm wide, the tube 9.3 mm long; stamens 5, the filaments 10.5 mm long, the upper 2.6 mm free, villose at and above insertion, the anthers oblong, 2 mm long; ovary oblong, 1.8 mm long, 1.1 mm broad, glabrous; disc small, not evidently distinct from the base of the ovary; style 5.3 mm long, the stylar branches 0.9 mm long, the stigma lobes clavate. Fruits seated in the cupulate calyx, drupaceous, glabrous, the stone slightly inequilaterally ovoid, 8.5–16.5 mm long, 6–7.5 mm broad, the endocarp bony.

Distribution. *Cordia anisophylla* occurs in wet forests from sea level to 1,000 m in elevation and is known only from Panama in the provinces of Colón, Darién, Panamá, and San Blas.

Cordia anisophylla is closely related to *C. panamensis* and to *C. cymosa* but differs from them by having corollas more than 10 mm long and fruits more than 8.5 mm long. This species is also one of only two distylous Central American members of sect. *Myxa*, the other being *C. dentata*. While the *Cordia panamensis* species complex is one of the most taxonomically confusing within sect. *Myxa*, *Cordia anisophylla* is probably the most distinctive species of the group in its elongate, distylous flowers and ellipsoid fruits.

Additional specimens examined. PANAMA. COLÓN: Santa Rita Ridge, *Croat 13895* (MO); Santa Rita lumber

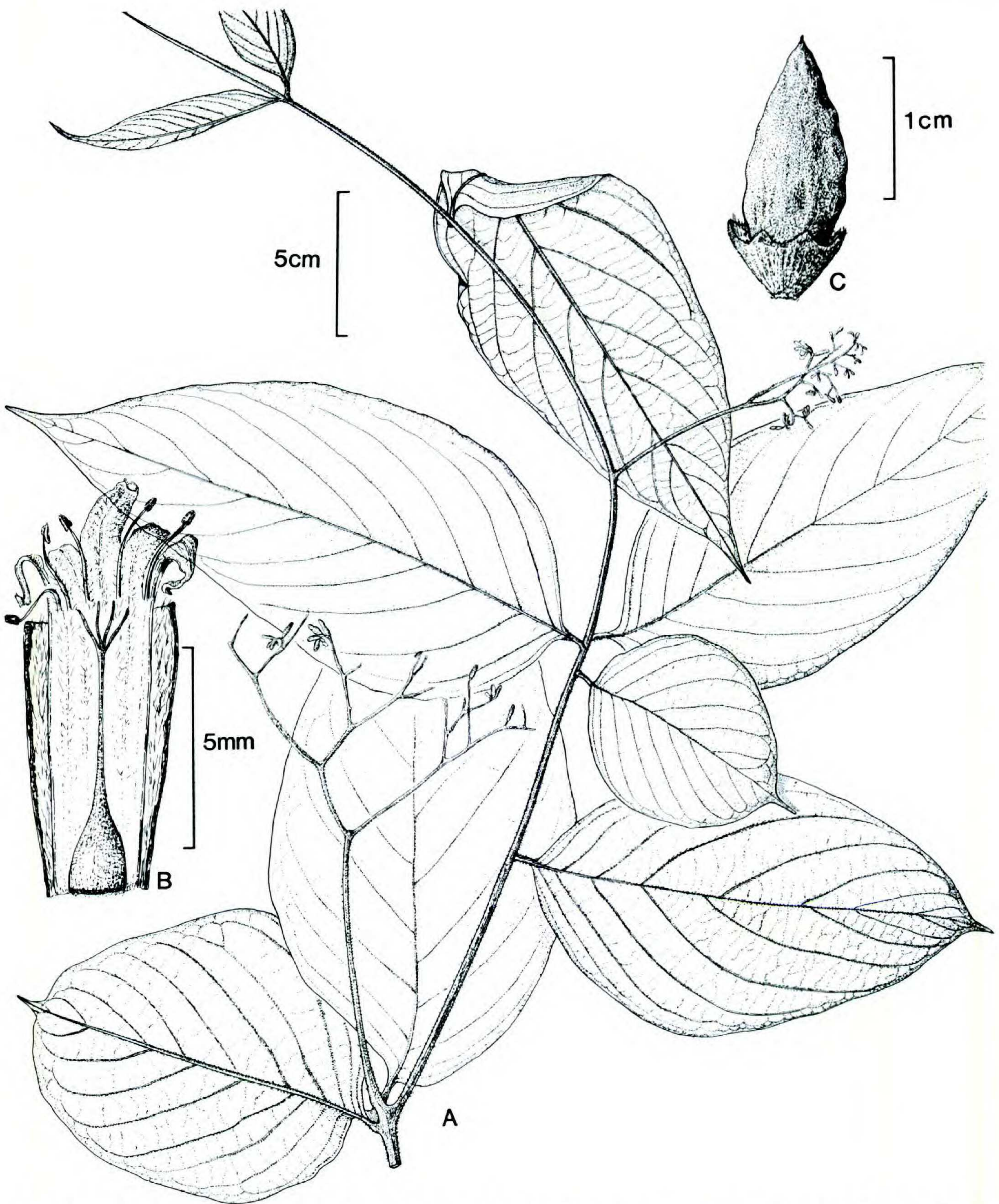


FIGURE 1. *Cordia anisophylla*.—A. Flowering branch.—B. Flower with corolla opened.—C. Fruit. A, B from Mori & Kallunki 5076 (MO), Colón, Panama; C from Mori & Kallunki 6373 (MO), Panamá, Panama.

road, ca. 15 km E of Colón, *Dressler* 3799 (DUKE, F (2), MO (2)); Santa Rita Ridge Road, ca. 8 mi. E of the Transisthmian Highway, along trail N of road, 350–440 m, *McPherson & Merello* 8244 (MO). DARIÉN: along Río Chucanaque between El Real and Río Canalones, *Duke* 4979 (MO). PANAMÁ: region of Cerro Jefe, 1,000 m, *Correa et al.* 1589 (MO); El Llano–Carti Road, 20.7 km from Interamerican Highway, 350 m, *Mori & Kallunki*

5114 (MO); 5–10 km NE of Altos de Pacora on trail at end of road, 700–800 m, *Mori & Kallunki* 6057 (DUKE); El Llano–Carti Road, 12.2 km from Interamerican Highway, *Mori & Kallunki* 6373 (MO, SCZ, US); El Llano–Carti Road, ca. 9 mi. from Pan-American Highway along newly cut by-pass, 300–400 m, *Sytsma* 4127 (MO). SAN BLAS: near Nusigandi on Llano–Carti Road, 300–350 m, *McPherson* 10796 (MO).

Cordia bicolor A. DC. in DC., Prodr. 9: 485. 1845. TYPE: Surinam: *Hostmann 406* (holotype, G-DC, not seen; microfiche, MO; isotype, P).

Cordia trichostyla Pittier, Contr. U.S. Natl. Herb. 18(6): 252. 1917. TYPE: Guatemala. Alta Verapaz: vicinity of Secanquim, 550 m, 30 Apr. 1905, *H. Pittier 189* (holotype, US 472845).

Cordia belizensis Lundell, Amer. Midl. Naturalist 29: 488. 1943. TYPE: Belize. Toledo: Monkey River, in high ridge between Swacey Branch and Waha-leaf Creek, 5 July 1942, *P. H. Gentle 4045* (holotype, MICH; isotypes, GH, NY).

Tree to 20 m tall, the young twigs velutinous to puberulent. Leaves persistent; petioles (2-)3-8(-16) mm long; blades elliptic to ovate or narrowly elliptic, (8-)10-19(-22) cm long, (3.3-)4-9(-11.5) cm wide, the apex acuminate, the base obtuse to rounded, the margin entire, the adaxial surface sparsely strigillose to scabrous, the abaxial surface pale, puberulent to strigillose. Inflorescence terminal or borne in the axils of branches, cymose, to 13(-20) cm long, 14(-28) cm broad, the branches velutinous. Flowers sessile, bisexual, monomorphic with the stamens as long or longer than the stigmas; calyx tubular-campanulate, (3.3-)3.6-4.3(-4.9) mm long, ribs absent, densely strigillose, the 5 lobes deltate to attenuate; corolla white, tubular with reflexed lobes, 6.2-7 mm long, 5-merous, the lobes oblong, (2.3-)2.7-3(-3.8) mm long, the tube (2.5-)3.6-4.6(-5) mm long, pubescent in the mouth; stamens 5, the filaments (3.8-)4.8-6(-6.4) mm long, the upper (1-)1.8-3 mm free, pubescent at the point of insertion, the anthers oblong, 1-1.6 mm long; ovary ellipsoid, 0.8-1.6 mm long, strigillose; disc crateriform, 0.3-1 mm tall; style 3-3.7 mm long, the stigma lobes discoid to broadly clavate. Fruits seated in the cupulate calyx, white, drupaceous, the stone inequilaterally ovoid, (7.3-)10.5-13 mm long, (4.5-)7.5-9.5 mm broad, the exocarp densely strigillose, the endocarp bony.

Distribution. *Cordia bicolor* occurs in wet forests from sea level to 500 m in elevation and ranges from Mexico to South America. In Panama this species is known

from the Canal Area, Chiriquí, Colón, Darién, Panamá, and Veraguas.

Cordia bicolor is perhaps most closely related to the *C. panamensis* complex in that it also has dichotomous lateral branching, anisophyllous leaves, and similar indument. However, it differs from the other Central American species in its strigillose fruits, a relatively rare character found in several unrelated South American species. *Cordia toqueve* Aubl. of South America is the only other species of this complex that shares this trait.

Additional specimens examined. PANAMA. CANAL AREA: Barro Colorado Island, *Aviles 21* (F); *Croat 5630* (DUKE, F, MO, NY, SCZ), *5823* (DUKE, F, NY, SCZ (2)), *7705* (DUKE, F, MO, NY), *8004* (F, MO, NY, SCZ), *8804* (DUKE, MO), *8809* (F (2), DUKE, MO, NY), *9447* (MO), *14855* (MO, SCZ, UC); *Duke 8379* (NY); without definite locality, *Epplesheimer s.n.* (F (2)); Barro Colorado Island, *Foster 1778* (DUKE, F); area W of Limón Bay, Gatún Locks and Gatún Lake, *Johnston 1588* (A); Barro Colorado Island, *Kenoyer 656* (US); Pipeline Road between mile marker 0 and 11.1 ca. 16 mi. N of Gamboa, *Lewis et al. 5446* (F, MO, NY); near Fort Randolph, *Maxon & Harvey 6520* (US); Barro Colorado Island, *Oppenheimer 252* (MO); near old Fort Lorenzo, mouth of Río Chagres, *Piper 5964* (US). CHIRIQUÍ: at Monte Rey above Boquete, *Croat 15770* (NY). COLÓN: near radio tower at the end of turnoff to Santa Rita Ridge Road, 200-300 m, *Miller & Miller 910* (MO). DARIÉN: ca. 1 mi. NE of Nura, 200 m, *Duke 10081* (MO, US). PANAMÁ: San José Island, *Erlanson 256* (G, NY, US); *Johnston 417* (GH), *545* (GH, MO, U, US), *618* (DUKE, GH, LL), *620* (GH, U, US), *621* (DUKE, GH, LL, U), *785* (GH, US), *963* (GH), *1076* (GH (2)); Altos del Río Pacora, 2,500 ft., *Lewis et al. 2267* (MO, UC). VERAGUAS: above Santa Fe on slopes of Cerro Tute below Agricultural School, *Gentry 6204* (MO); NW of Santa Fe near entrance to school, *Mori & Kallunki 4888* (AAU, MO, US).

Cordia bifurcata Roemer & Schultes, Syst. Veg. 4: 466. 1819. *Varronia dichotoma* Ruíz Lopez & Pavón, Fl. Peruv. 2: 23, t. 146. 1799, not *Cordia dichotoma* G. Forster, Fl. Ins. Austr. 18 n. 110. 1786. TYPE: Peru. Huánuco: Chacahuasi, *Hipólito Ruíz & José Pavón s.n.* (holotype, B-W, not seen; microfiche, MO).

Shrub to 3 m tall, the twigs sparsely strigillose, the hairs shorter than 0.5 mm, appressed, white translucent. Leaves deciduous,

on short spurs 1.5–2 mm long; petioles 2–8 mm long, sparsely strigillose; blade ovate to lanceolate, (2.5–)3.7–9(–12) cm long, (0.8–)1.2–4(–4.7) cm wide, the apex acuminate, the base acute, the margin slightly serrate to entire, the adaxial surface sparsely puberulent with short, erect hairs, the abaxial surface sparsely pubescent. Inflorescence terminal or lateral, a small forking cyme with 4 or more branches, 0.8–2.3 cm broad, the peduncle 1.4–6 cm long, strigillose. Flowers sessile, distylous; calyx short-tubular, 2–2.7 mm long, strigillose, the 5 lobes deltate to shallowly deltate; corolla white, tubular, (2.7–)3.2–3.7 mm long, truncate at the apex, canescent in the middle of the tube; stamens 5, the filaments (2.2–)2.7–3.5 mm long, the upper 0.6–1(–1.3) mm free, canescent at insertion, the anthers broadly ellipsoid, 0.5–0.6 mm long; ovary very broadly obovoid to broadly depressed obovoid, 0.6–1 mm long; disc thin, cuplike, nearly completely adnate to the ovary; style (2.2–)3–3.5 mm long, the stigma lobes flattened. Fruits drupaceous, $\frac{1}{3}$ – $\frac{1}{2}$ enclosed in the slightly accrescent calyx, bright red, the stone ovoid, 4–4.5 mm long, 2.2–3 mm broad, the endocarp bony.

Distribution. *Cordia bifurcata* occurs in wet forests from sea level to 600 m in elevation and ranges from southern Nicaragua south to Peru. In Panama this species is known from the provinces of Bocas del Toro, Colón, and Darién.

Cordia bifurcata is distinctive in its small, shrubby habit and small, cymose inflorescences and has no close relatives in Panama. It is a member of a taxonomically difficult group of mostly South American species that are all similar in general aspect. The only other member of this group found in Central America is *C. foliosa* Mart. & Gal. of southern Mexico and Guatemala, which differs from *C. bifurcata* in its elliptic, firm-textured leaves with a scabrous upper surface, apiculate flower buds, and acuminate calyx lobes. Two other species of Central America, *C. inermis* and *C. linnaei*, are also closely related to this

group, but neither of these has a branched inflorescence.

Additional specimens examined. PANAMA. BOCAS DEL TORO: region of Almirante, *Cooper 83* (F, NY); Changuinola Valley, *Dunlap 90* (GH). COLÓN: vicinity of San Juan near Cement Plant Lake, *Blum & Tyson 537* (MO). DARIÉN: on trail from Punta Guayabo Grando to Río Jaqué, 50–200 m, *Antonio & Hahn 4415* (MO); vicinity of Paya, Río Paya, *Stern et al. 268* (G, MO, US).

Cordia bullata (L.) Roemer & Schultes, *Syst. Veg.* 4: 462. 1819. *Varronia bullata* L., *Syst. ed.* 10: 916. 1759. TYPE: Jamaica, *P. Browne s.n.* (holotype, LINN, not seen (Savage Catalog number 255.2); microfiche, MO).

Cordia bullata var. *angustata* DC., *Prodr.* 9: 496. 1845. TYPE: Guadalupe, 1818, *Krause s.n.* (holotype, G-DC, not seen; microfiche, MO).

Cordia asperrima DC., *Prodr.* 9: 498. 1845. *Varronia asperrima* (DC.) Friesen, *Bull. Soc. Bot. Genève*, Ser. 2, 24: 155, t. 1, f. 5. 1933. TYPE: Jamaica, 1822, *Bertero ex herb. Balbis* (holotype, G-DC, not seen; microfiche, MO).

Shrub to 1(–3) m tall, the twigs hirsute to hirtellous, the hairs erect to spreading. Leaves deciduous, on short spurs to 1 mm long; petioles 2–7(–10) mm long, shallowly canalliculate to flattened adaxially, hirsute to hirtellous, the hairs erect to spreading; blade ovate to narrowly ovate, (1.5–)2–8(–9.2) cm long, (0.8–)1.2–4.7(–6.3) cm wide, the apex acute to slightly attenuate, the base subobtuse to obtuse or acute and abruptly decurrent along the petiole, the margin serrate, usually unevenly so, the teeth usually sharp and often short-apiculate, the adaxial surface usually bullate, strigose, the lower surface coarsely pubescent, the hairs \pm restricted to the veins. Inflorescence internodal or less commonly subterminal or terminal, a dense, often slightly ellipsoid head, 8–12(–15) mm broad, the peduncle (1.5–)3–6.5(–13.5) cm long, hirsute, the hairs erect to spreading. Flowers distylous, sessile; calyx campanulate, (2–)2.5–3.3(–3.8) mm long, (2–)2.5–3.5 mm wide at the mouth, ribs absent, strigillose, the 5 lobes deltate to triangular, 0.5–1 mm long, with a prolonged filiform tip 1–3(–3.5) mm long; corolla white, tubular, 3–5.3(–6) mm long,

undulate, the lobes scarcely distinct, the tube 1.2–2.8 (–3.2) mm long; stamens 5, the filaments (3.3–) 3.8–4.3(–5) mm long, the upper 1–1.7(–2) mm free, puberulent in a ring in the mouth of the corolla tube, the anthers ellipsoid, 0.6–1 mm long; ovary ovoid, 1–1.8 mm long, glabrous; disc usually indistinct from the base of the ovary; style 0.6–4.3 mm long, the stylar branches 0.4–1 mm long, the stigma lobes clavate to discoid. Fruits drupaceous, red, the stone ovoid, 3.7–5.3 mm long, 2.5–3.2 mm broad, the mesocarp thin, the endocarp bony.

Distribution. *Cordia bullata* occurs in dry forests from sea level to 1,400 m in elevation. It is known from Nicaragua to southern Mexico, northern South America, the Greater Antilles, and a single collection from the province of Veraguas in Panama.

Cordia bullata is closely related to and often confused with *C. globosa* (Jacq.) Kunth but differs by having peduncles greater than 3 cm long and corollas less than 6 mm long. Both are common in northern Central America, and populations with interspecific hybrids are known from Nicaragua and Honduras.

Additional specimens examined. PANAMA. VERAGUAS: El Cuchillo, near Cerro Tute, up from Santa Fe, 1,300 m, *Hamilton et al.* 1203 (MO).

***Cordia collococca* L., Sp. Pl. ed. 2. 274. 1762; excluding *Cordia glabra* L. = *Bourreria succulenta* Jacq.; I. M. Johnston, J. Arnold Arbor. 21: 345. 1940. TYPE: without definite locality, collector unknown (holotype, LINN, not seen (Savage Catalog number 253.8); microfiche, MO).**

Cordia micrantha Sw., Prodr. 47. 1788. TYPE: "habitat in Jamaica," not seen.

Small tree to 8(–15) m tall, the twigs sparsely to evenly strigillose, later waxy. Leaves deciduous; petioles 5–12(–15) mm long, sparsely strigillose; blade oblong-obovate to elliptic or obovate, (4.7–)5.5–14(–15.2) cm long, (2.5–)3–6.5(–7) cm wide, the apex acute, often with short-acuminate tip, rarely acute, the base cuneate to acute, the margin

entire, the adaxial surface glabrous or nearly so but with numerous small papillae, the abaxial surface evenly strigillose to hirtellous. Inflorescence terminal, borne on old wood just before the new vegetative shoots appear, or axillary, cymose, (6–)7–14(–18) cm broad, the branches sparsely strigillose. Flowers sessile, unisexual by abortion, the plants dioecious; female flowers with small, nonfunctional anthers; male flowers with shortened, reduced styles; calyx cupulate, (1.7–)2–2.6 (–3) mm long, ribs absent, evenly strigillose, circumscissile or unevenly 3-lobed; corolla white, tubular with reflexed lobes, (4.5–)4.8–6.3(–6.9) mm long, 5-merous, the lobes oblong-ovate to ovate, (2.3–)2.8–3.7(–4) mm long, the tube 1.7–2.9(–3.3) mm long; stamens 5, the filaments 2.5–5 mm long, the upper (0.8–)1.7–2.2 mm free, puberulent to pubescent below insertion, the anthers oblong to ellipsoid, 0.5–1.6 mm long; ovary ovoid to oblong, 0.8–1.2 mm long, glabrous; style 0.4–2 mm long, the stigma lobes clavate to filiform. Fruit borne with the small calyx persisting at the base, bright red, drupaceous, glabrous, the stone inequilaterally ovoid, 7.5–9.3 mm long, 5.5–7.3 mm broad, the endocarp bony.

Distribution. *Cordia collococca* occurs in dry forests from sea level to 200(–900) m in elevation from Mexico south to northern South America and the West Indies. In Panama this species is known from Bocas del Toro, Canal Area, Chiriquí, Colón, Herrera, Los Santos, Panamá, and San Blas.

Cordia collococca is a relatively common species throughout much of its range, although it has not been collected frequently in Panama. It is easily confused with *Cordia eriostigma* but can be distinguished by being a smaller tree with an even indument of short appressed hairs on its abaxial leaf surface, deciduous leaves, and flowers that are unisexual by abortion. *Cordia collococca* is generally found at elevations below 200 m in dry forests, while *C. eriostigma* usually grows at 600–1,400 m in moist forests.

Cordia micrantha is clearly a synonym of *C. collococca*, but Swartz specified no type

other than "habitat in Jamaica," and the choice of a lectotype will require study of material in European herbaria. The name *Cordia glabra* has been improperly applied to this species; Johnston (1940) showed that this name should be considered a synonym of *Bourreria succulenta*.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Almirante, *Cooper 406* (CFMR, F, NY, US); on lower Changuinola River, *Stork 273* (UC, US). CANAL AREA: between Farfan beach and Vera Cruz, *Duke 11733* (MO). CHIRIQUÍ: Progreso, *Cooper & Slater 300* (CFMR, F, US); without definite locality, *Cooper & Slater 307* (CFMR, F, NY, US). COLÓN: Santa Rita Ridge, 500 m, *McPherson 8456* (MO). HERRERA: carretera a Pesé, *Lao 585* (MO). LOS SANTOS: Punta Mala, *Croat 9756* (DUKE), *9763B* (MO (2)). PANAMÁ: vicinity of Pacora, 0–20 m, *Allen 3455* (BM, BR, F, G, MO); cerca del Río Chame, *Moron 28* (MO). SAN BLAS: Permé, *Cooper 235* (NY, US).

Cordia correae James S. Miller, sp. nov.

TYPE: Panama. Coclé: La Mesa, 4 km north of El Valle, disturbed tropical wet forest and roadside, 875 m, 3 Jan. 1974, *M. Nee & J. D. Dwyer 9164* (holotype, MO 2414635; isotype, DUKE). Figure 2.

Arbor vel frutex ad 8 m alta, ramunculis glabris ad strigillosis. Folia persistentia, petiolis 5–10(–14) mm longis, strigillosis; laminae anisophyllae, coriaceae, foliis maioribus ovatis ad anguste ovatis, 10.3–17.6 cm longis, 4.8–8.8 cm latis, apice acuminatis, basi rotundatis ad obtusis, superficie sparsim strigillosa, pagina inferiore minute strigillosa. Inflorescentiae internodales vel axillares, cymosae, ad 5.5 cm latae. Flores sessiles; calyx urceolatus, 5.6 mm longus, rufostrigillosus. Fructus drupaceus, aurantiacus, putamine inaequaliter ovoideo, 8.4–13 cm longo, 6.2–9 mm lato, ruminato.

Tree or shrub 4(–8) m tall, the twigs nearly glabrous to strigillose. Leaves persistent; petioles 5–10(–14) mm long, canaliculate adaxially, unevenly and often sparsely strigillose; blades anisophyllous, coriaceous, the larger ones ovate to narrowly ovate, 10.3–17.6 cm long, 4.8–8.8 cm wide, the smaller ones ovate, 7–8 cm long, 4–5.5 cm wide, the apex acuminate, the base rounded to obtuse or rarely acute, the margin entire, the adaxial surface with widely scattered appressed hairs, the abaxial surface minutely strigillose. Inflorescences subterminal, internodal or axillary, few per stem, cymose, to 5.5 cm broad, expanding somewhat in fruit, peduncle 1.8–5.3 cm long,

strigillose, the hairs brown. Flowers sessile; calyx urceolate, 5.6 mm long, 3 mm wide at the mouth, the 5 lobes deltate, 0.7–1.4 mm long, ribs absent, rufous-strigillose; corolla white, tubular with reflexed lobes, 8.5 mm long, 5-merous, the lobes oblong, 3.6 mm long, 1.9 mm wide, the tube 7.8 mm long; stamens 5, the filaments 10.5 mm long, the upper 6 mm free, glabrous, the anthers oblong, ca. 1 mm long; ovary ovoid, glabrous; style ca. 4 mm long, the stylar branches 2.3 mm long, the stigma lobes clavate. Fruits borne in the slightly expanded, saucer-shaped calyx, orange at maturity, drupaceous, glabrous, the stone inequilaterally ovoid, 8.4–13 mm long, 6.2–9 mm broad, ruminant, the endocarp bony.

Distribution. *Cordia correae* occurs in wet forests from 800 to 1,000 m in elevation and is known only from Panama in the provinces of Coclé, Panamá, and Veraguas.

Cordia correae is known from only a few collections from Panama in the region of El Valle and from Cerro Jefe. Its closest relative is probably *C. protracta* I. M. Johnston, a species of low elevations along the Atlantic coast of San Blas and adjacent Colombia. The two species share similar habits of growth, branching patterns, anisophyllous leaves, and distinctly five-lobed calyces. The fruits of *C. correae*, however, are orange, subglobose, and have a ruminant surface, while those of *C. protracta* are white, elongate, and ridged longitudinally. *Cordia correae*, which is endemic to Panama, is named in honor of Profesora Mireya D. Correa A., who has done much to advance the study of Panamanian plants.

Additional specimens examined. PANAMA. COCLÉ: La Mesa above El Valle, along road which ends in pasture, 810 m, *Croat 25310* (MO, NY); vicinity of La Mesa, N of El Valle, 1,000 m, *Gentry 6813* (AAU, MO, NY); Cerro Pilón, El Valle Site Area of WEPCOR, *Kirkbride 1071* (NY); La Mesa, 4 km N of El Valle, 850–875 m, *Nee & Dwyer 9214* (MO (2), NY). PANAMÁ: along road, 18.9 km N of Cerro Azul, *Mori & Kallunki 4998* (AAU, DUKE, NY, (2)). VERAGUAS: vicinity of Cerro Tute, forested slopes along trail to summit, 850–1,000 m, *McPherson 10684* (MO).

Cordia croatii James S. Miller, sp. nov.

TYPE: Panama. Veraguas: 5 mi. west of

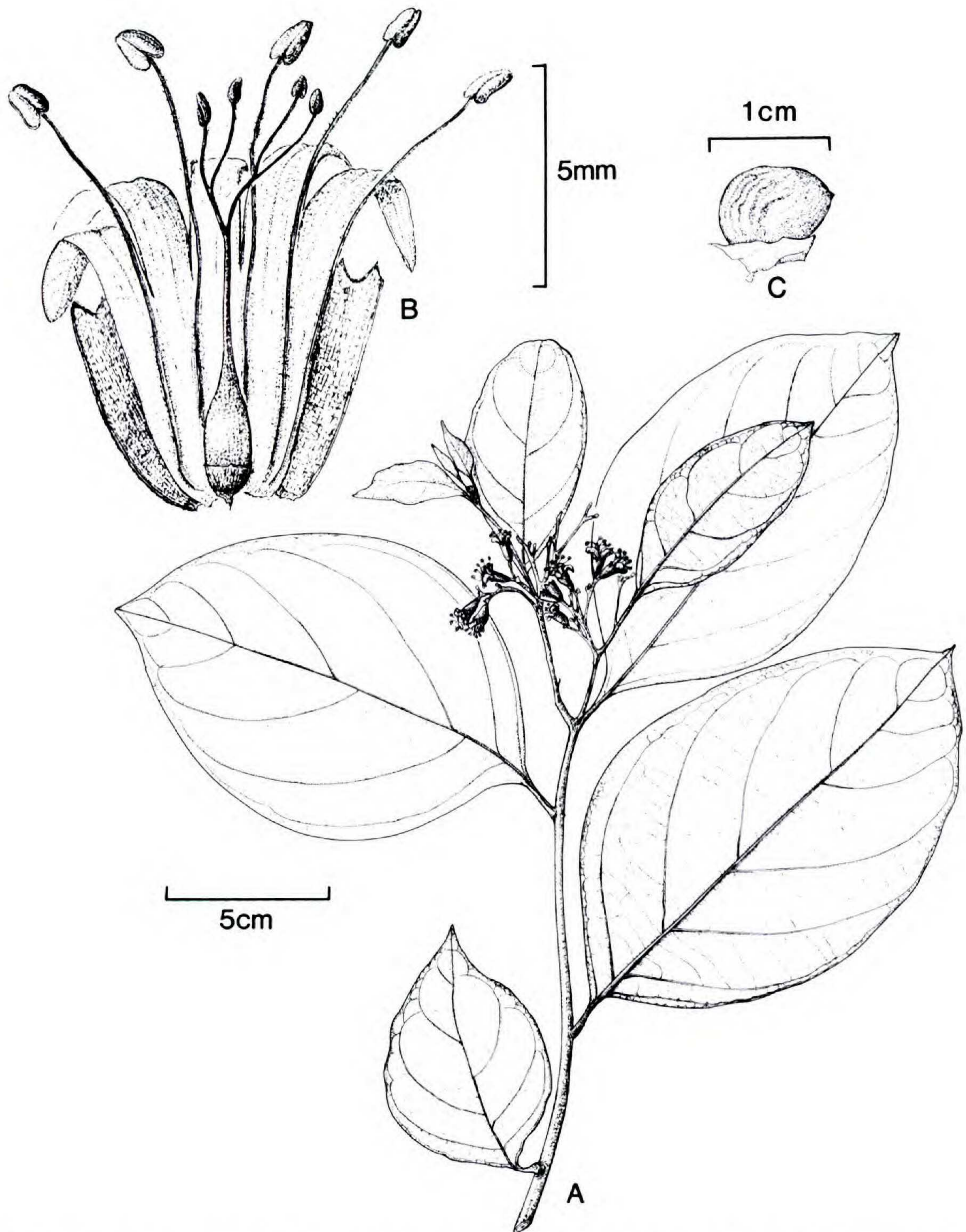


FIGURE 2. *Cordia correae*.—A. Flowering branch.—B. Flower with calyx and corolla opened.—C. Dried fruit. A, B from Nee & Dwyer 9164 (MO), Coclé, Panama; C from Mori & Kallunki 4998 (NY), Panamá, Panama.

Santa Fe on road past Escuela Agricola Alto Piedra on Pacific side of divide, 800–1,200 m, *T. B. Croat 23059* (holotype, MO 2198065; isotypes, AAU, BR, C, CAS, CR, DUKE, F, L, LL, MEXU, NY, RSA, US, WIS). Figure 3.

Arbor ad 20 m alta, ramunculis glabris ad strigillosis. Folia persistentia, petiolis 6–12 mm longis, laminae ellipticae ad elliptico-ovatae, (4.5–)5.7–8.2(–11.2) cm longae, (2–)3–4.3(–4.8) cm latae, apice acuto ad leviter acuminato, basi acuta ad obtusa. Inflorescentiae termi-

nales, cymosae (3–)8–12(–15) cm latae. Flores bisexuales; calyx campanulatus, 3–4.3 mm longus, glaber, 3(–4)-lobatus; corolla alba, tubularis, 5–7.2 mm longa, 5-lobata, lobis reflexis, ovatis; stamina 5, filis 4–6.5 mm longis, villosis, antheris oblongis, 1.1 mm longis. Fructus drupaceus, putamine inaequaliter ovoideo, 8–11 mm longo, 6–8(–11) mm lato.

Tree to 20 m tall, the twigs nearly glabrous to sparsely strigillose, often with considerable waxy deposits. Leaves persistent; petioles 6–12 mm long, deeply canaliculate adaxially, nearly glabrous to sparsely strigillose; blades

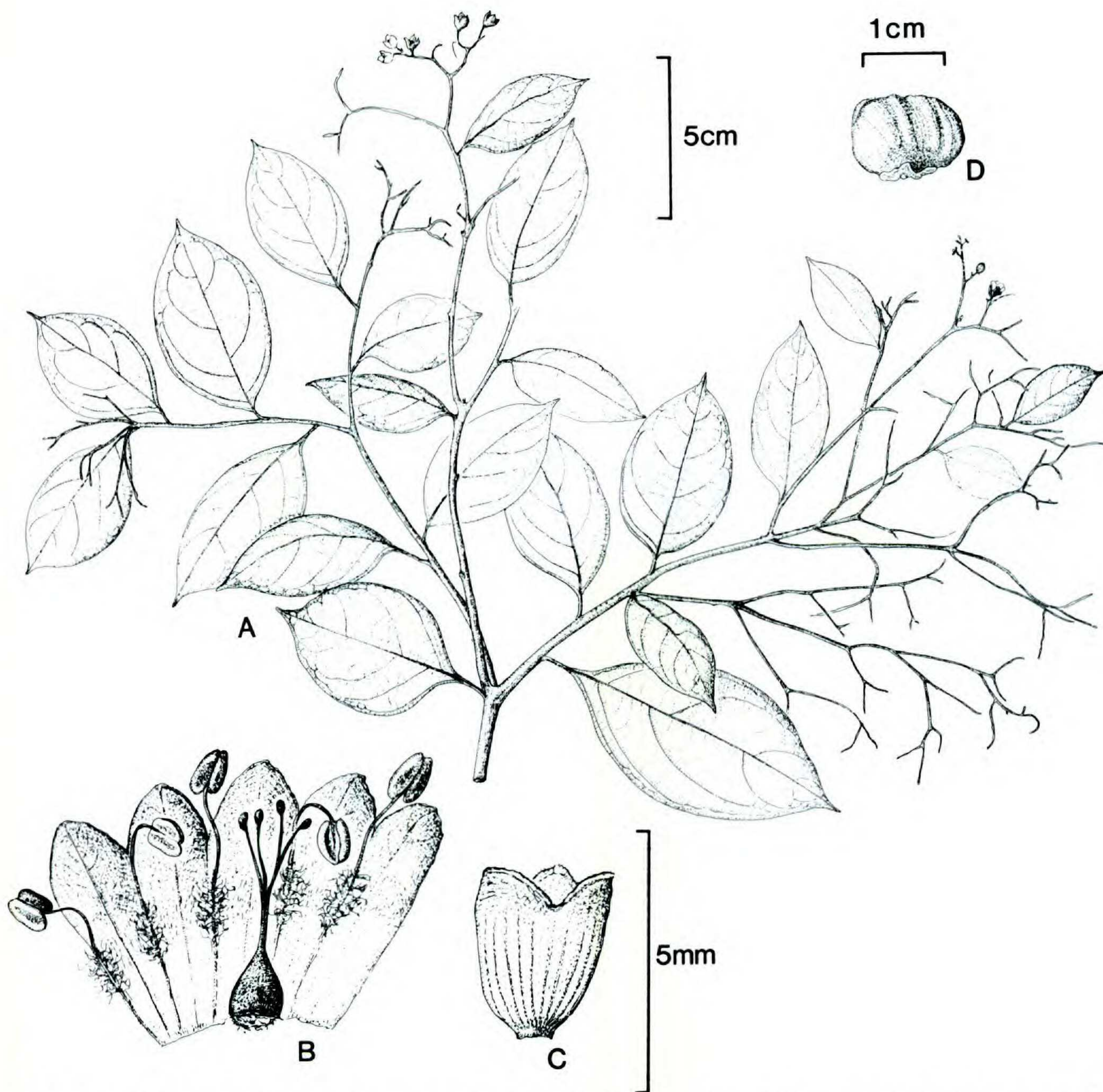


FIGURE 3. *Cordia croatii*.—A. Flowering branch.—B. Flower with corolla opened.—C. Calyx.—D. Dried fruit.—A–C from Croat 23059 (MO), Veraguas, Panama; D from Tonduz 12520 (US), Alajuela, Costa Rica.

elliptic to elliptic-ovate, (4.5–)5.7–8.2(–11.2) cm long, (2–)3–4.3(–5) cm wide, the apex acute to slightly acuminate, the base acute or less commonly obtuse and slightly decurrent, the margin entire, the adaxial surface glabrous to papillose with widely scattered appressed hairs, the abaxial surface glabrous. Inflorescence terminal, cymose (3–)8–12 (–15) cm broad, the branches sparsely brown-strigillose to ferruginous-puberulent. Flowers sessile, monomorphic, the stamens longer than style; calyx campanulate, 3–4.3 mm long, 3.4–4 mm wide at mouth, the 3(–4) lobes ovate, rounded at apex, 1–1.8 mm long, ribs absent, glabrous; corolla white, tubular with

reflexed lobes, 5–7.2 mm long, 5-merous, the lobes ovate, 2–4.3 mm long, 1.5–3 mm wide, the tube 2.2–3 mm long, glabrous; stamens 5, the filaments 4–6.5 mm long, the upper 2–2.5 mm free, villous along the lower free portion, the anthers oblong, 1.1 mm long; ovary ovoid to conical, 1–1.6 mm long, 1–1.4 mm broad, glabrous; disc crateriform, 0.4–0.5 mm tall, 1–1.1 mm broad, glabrous; style 2–2.3 mm long, the stylar branches 1.7–2.5 mm long, the stigma lobes discoid. Fruits borne in the saucer-shaped calyx, drupeaceous, glabrous, the stone inequilaterally broadly ovoid, 8–11 mm long, 6–8(–11) mm broad, the endocarp bony.

Distribution. *Cordia croatii* occurs in cloud forests from 800 to 1,200 m in elevation and is known from the San Ramón region of Costa Rica and the provinces of Coclé and Veraguas in Panama.

Cordia croatii is distinct in its small elliptic leaves. It is known only from a few Panamanian collections and several from the San Ramón region of Costa Rica, although further collecting efforts may reveal it in cloud forests in between. This species is somewhat unusual in sect. *Myxa* in that it occurs at relatively high elevations, unlike the majority of its relatives, which are usually found in lowland wet forests. *Cordia croatii* shares a three-lobed calyx with *Cordia lasiocalyx* Pittier, *C. lucidula* I. M. Johnston, and *C. porcata* Nowicke and is probably closely related to these species. *Cordia croatii* is named in honor of Dr. Thomas B. Croat who collected the type material and has contributed greatly to the study of Panamanian botany.

Additional specimens examined. PANAMA. COCLÉ: Cerro Pilón, 2,900 ft., *Lallathin 1F* (MO); *1-1* (MO).

Cordia curassavica (Jacq.) Roemer & Schultes, *Syst. Veg.* 4: 460. 1819. *Varronia curassavica* Jacq., *Enum. Syst. Pl.* 14. 1760. TYPE: Curassao, *Jacquin* (not seen).

Cordia obliqua Kunth in Humb., *Bonpl. & Kunth, Nov. Gen. Sp.* 3: 74. 1818. *Cordia peruviana* var. *mexicana* DC., *Prodr.* 9: 491. 1845. TYPE: Mexico. Campeche: *collector unknown* (holotype, P, not seen; microfiche, MO).

Cordia brevispicata Martens & Galeotti, *Bull. Acad. Roy. Sci. Bruxelles* 11(2): 331. 1844. TYPE: Mexico. Puebla: Tehuacán, Apr. 1840, *Galeotti 7192* (holotype, BR; isotypes, BR, G, K).

Cordia linearis A. DC., *Prodr.* 9: 493. 1845. TYPE: Mexico: *Herb. Pavón* (holotype, G-DC, not seen; microfiche, MO).

Cordia hispida Benth., *Bot. Voy. Sulphur* 139. 1845. TYPE: Honduras: Gulf of Fonseca, *Sinclair s.n.* (holotype, K).

Cordia palmeri S. Watson, *Proc. Amer. Acad. Arts* 24: 62. 1889. TYPE: Mexico. Sonora: Guaymas, 1887, *E. Palmer 281* (holotype, GH; isotypes, C, K, NY, UC, US (3)).

Cordia socorrensis Brandegees, *Erythea* 7: 5. 1899. TYPE: Mexico. Colima: Socorro Island, Mar.–June 1897, *Anthony 384* (holotype, UC 78381; isotypes, DS, F, GH, K, MEXU, MO, POM, SD, US).

Cordia brevispicata var. *hypomalaca* Greenman, *Publ. Field Columbian Mus., Bot. Ser.* 2: 338. 1912. TYPE: Mexico. Oaxaca: Cerro San Filipe, 1,700 m, 30 June 1907, *Conzatti 1831* (lectotype, here designated, F 225986; isolectotypes, F, GH). In describing this variety Greenman designated Conzatti's collection at the Field Museum as the type and listed two accession numbers (225986 and 246873). Neither sheet had been clearly marked as holotype by Greenman, and the better of the two specimens is selected as a lectotype here to rectify this situation.

Cordia imparilis J. F. Macbr., *Contr. Gray Herb.* 49: 16. 1917. TYPE: Mexico. Michoacán or Guerrero: 1 Aug. 1898, *E. Langlasse 265* (holotype, GH; isotypes, G (2), K, US).

Cordia chepensis Pittier, *Contr. U.S. Natl. Herb.* 18: 253. 1917. TYPE: Panama. Panamá: Chepo, 60 m, Oct. 1911, *H. Pittier 4511* (holotype, US 679672; isotype, US).

Cordia littoralis Pittier, *Contr. U.S. Natl. Herb.* 18: 253. 1917. TYPE: Costa Rica. Limón: Porto Limón, 27 May 1911, *H. Pittier 3641* (holotype, US 678699; isotype, GH).

Cordia mollis Pittier, *Contr. U.S. Natl. Herb.* 18: 294. 1917. TYPE: Guatemala: between Chiguin and Trapiche Grande, 900 m, 19 Apr. 1905, *H. Pittier 134* (holotype, US 472788).

Shrub to 2(–4) m tall, the twigs glabrous to strigillose or puberulent or rarely hirsute but always with small, globose wax particles. Leaves deciduous, on short spurs to 1 mm long; petioles 1–8(–21) mm long, strigillose or puberulent to hirsute; blades lanceolate to narrowly elliptic or elliptic-ovate, (1–)2–9.4 (–16) cm long, 0.5–4(–7.3) cm wide, the apex acute, the base cuneate to acute and sometimes decurrent, the margin serrate, occasionally merely undulate, the adaxial surface scabrous to papillose, the abaxial surface strigillose with most hairs restricted to the major veins, or tomentulose. Inflorescence terminal, spicate, 1.5–8.8(–15) cm long, the peduncle 1.8 cm long, puberulent or strigillose to nearly glabrous. Flowers sessile, distylous; calyx campanulate, 2–3.2(–3.8) mm long, the 5(–6) lobes deltate; corolla white, tubular with reflexed to spreading lobes, (3.8–)4.8–6.8 (–8.2) mm long, 5(–6)-merous, the lobes ovate to depressed ovate, 1.2–1.8(–2.8) mm long, the tube 2.4–3.4 mm long; stamens 5, the filaments 3.2–5(–6) mm long, the upper 0.8–2 mm free, the free portion glabrous, puberulent to pubescent beneath the point of insertion, the anthers el-

lipoid, (0.3–)0.7–1 mm long; ovary ovoid to broadly ovoid, (0.8–)1–1.2(–1.6) mm long; disc crateriform, 0.4–0.6(–0.8) mm tall; style (1.4–)2–4(–5.7) mm long, the stigma lobes clavate. Fruits drupaceous, red, $\frac{1}{2}$ – $\frac{3}{4}$ enclosed in the slightly accrescent calyx, the stone ovoid, (3.7–)4–4.5 (–6) mm long, 2.2–3 mm broad, the endocarp bony.

Distribution. *Cordia curassavica* is common in a wide variety of habitats but is found most often in disturbed or dry areas from sea level to 2,000 m in elevation. This species ranges from Sonora and Baja California in northern Mexico south to northern South America and east to the West Indies. It is known from all of the provinces in Panama.

Cordia curassavica is extremely variable, and many of its variants have been recognized as taxonomically distinct by previous authors. Much of the variation throughout the range of *C. curassavica* is in overall size of the plants, size of leaves, and size of inflorescences. Individuals from populations in Baja California and Socorro Island are quite small in stature with leaves much reduced in size; the synonym *C. socorrensis* Brandegees is based on a collection of this sort. The most diminutive plants occur in populations from the Tehuacán region of Puebla, Mexico, the area from which the type of another synonym, *Cordia brevispicata* Martens & Galeotti, was collected.

The other extreme variant of *Cordia curassavica* occurs along the Atlantic coast of Central America, and only in Panama can it be found on the Pacific slope. These plants are more robust and differ from other populations in being larger in all aspects as well as in having broader leaves. Also, the pubescence of the upper leaf surface differs from what is seen in other populations; the hairs are represented only by the persistent bases, lacking shafts. *Cordia chepensis*, based on a type collection from Chepo, and *Cordia littoralis*, based on a population from the Atlantic coast of Costa Rica, are synonyms of this sort. These were referred to as “typical

Cordia curassavica” by Johnston (1949a), who felt that with further study, several segregate species would be recognized. Numerous collections from all portions of the range indicate that there are no clear morphological discontinuities.

Although populations of *Cordia curassavica* vary over its geographic range, a much greater component of this variation appears to be due to phenotypic response to local climate rather than genetic differences between the populations. While collections made in the field from different regions often vary widely in appearance, most of these differences are not evident in the plants that have been raised in the greenhouse from seed collected in Mexico, Nicaragua, and Panama. Adult plants raised from seed under uniform conditions from morphologically and geographically diverse populations are often virtually indistinguishable.

Cordia curassavica hybridizes with *C. spinescens* L. and with *C. bullata* (L.) Roemer & Schultes and probably hybridizes with several additional species (Miller, in prep.). Observations made on numerous hybrids show that they vary in pollen stainability according to the parentage, but even if sterile, they are capable of persisting by spreading rhizomatously. As a result, these hybrids are represented in herbarium collections, leading to confusion and the long list of synonyms associated with this species. Although interspecific hybridization appears to be relatively uncommon, it may be adding to the variability of populations through rare backcrossing to parent plants.

Data indicate that *Cordia curassavica* is best treated in a broad sense, as much of the variability between populations is phenotypic. While there are considerable differences between the extremes, none of the intermediates exhibit any significant reduction in pollen stainability. Despite this variability, *Cordia curassavica* is a well-marked species easily distinguished from *C. spinescens* by having lanceolate leaves and elongate, terminal, spicate inflorescences. *Cordia curassavica* differs from *Cordia guanacastensis* Standley,

the other Central American species with which it could be confused, by having much more elongate spikes generally less than 8 mm broad and by having the peduncles nearly glabrous or puberulent to strigillose rather than hispid as in *C. guanacastensis*.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Santa Catalina River bank and beach, *Blackwell et al.* 2710 (MO, SCZ, UC); vicinity of Almirante, Changuinola Canal, *Blum* 1389 (MO, SCZ); Chiriquí Lagoon, Isla Colón, 0–120 m, *Wedel* 562 (GH, MO, U), 2478 (MO, NY, US); Chiriquí Lagoon, Columbus Island, *Wedel* 2608 (MO, US); Chiriquí Lagoon, Isla Colón, *Wedel* 2923 (MO, NY, US). CANAL AREA: Ancon Hill, *Bartlett & Lasser* 16312 (GH, MICH, MO); Fort Sherman area, *Blum et al.* 386 (MO, SCZ); Gamboa Navy Pipe Line along main dirt road, *Correa & Haines* 541 (MO); road S-10, north of Escobal, *Croat* 12447 (F, MO); near beach at Fort Kobbe, *Duke* 4196 (MO (2)); near Coco Solo Weather Station, *Duke* 4284 (MO); Summit Gardens, *Dwyer* 7190 (MO); Fort San Lorenzo, *Ebinger* 457 (F, MEXU, MO); Ancon Hill, 100–200 m, *Killip* 12059 (GH, NY, US), 12106 (US); near Fort Randolph, *Maxon & Harvey* 6506 (US); low woods E of Bella Vista, a suburb of Panama City, *Maxon & Valentine* 6945 (US); Toro Point near Fort Sherman, *McDaniel* 4996 (MO); Fort San Lorenzo, bluff above Chagres River, *McDaniel* 5179 (MO); Curundu, 30–40 m, *Miller* 1033, 1034, 1035, 1036, 1037, 1038, 1039, 1040, 1041, 1042, 1043, 1044 (MO); along Fort Sherman road (S2 or 82), *Mori & Kallunki* 2712 (MO); Ancon Hill, *Standley* 25207 (US); Balboa, *Standley* 25552, 27152 (US); near Fort Randolph, *Standley* 28604 (US); Mount Hope Cemetery, *Standley* 28786 (US); vicinity of Fort Sherman, *Standley* 31220 (US); Fort Sherman near road to Gatún, *Tyson & Dwyer* 1206 (MO, SCZ); Howard Air Force Base near Red Devil drop zone, *Tyson* 1865 (MO); Fort Clayton, *Tyson et al.* 2304 (NY); vicinity of Miraflores Lake, just outside Naval reserve, *White* 244 (MO, NY). CHIRIQUÍ: along trail north of Cerro Punta, *Croat* 10477 (MO, NY). COCLÉ: vicinity of El Valle, 800–1,000 m, *Allen* 100, 753 (F, MO); hills S of El Valle de Antón, 700 m, *Allen* 2510 (US (2)); Río Hato Airstrip, *Blum & Dwyer* 2474 (AAU, SCZ); *Burch et al.* 1148 (K, MO, UC, US); 10 km W of Agua Dulce on the Interamerican Highway, *Correa* 87 (MO, SCZ); 3 mi. NE of Antón, *Croat* 9618 (MO, SCZ); road from Pan-American Highway to El Valle, 100–1,000 m, *D'Arcy & Sytsma* 14647 (MO); savannas near El Valle, *Duke & Mussell* 6615 (MO); Penonomé, *Dwyer* 2000 (MO (2)); along El Valle de Antón, 1 km up road toward La Mesa near first waterfall, *Folsom & Kauke* 2753 (MO); W of Río Guias, *Gentry* 5845 (MO); E facing slopes of the crater around El Valle de Antón, about 2 mi. W of town, 1,000 m, *Luteyn* 1245 (F, GH, MO); along the road to El Valle between the Pan-American Highway and El Valle, 400 m, *Miller et al.* 773 (MO); Agua Dulce, *Pittier* 4860 (NY, US); Río Grande en Coclé, *Rosario* 20 (F); El Valle de Antón and vicinity, 500–700 m, *Seibert* 439 (F, MO); 3–6 km SE of El Valle de Antón, *Wilbur & Luteyn* 11765 (DS, GH, LL, MICH, MO, NY, RSA, US); between Agua Dulce and Antón, 15–50 m, *Woodson et al.* 1207

(F, MO, NY); between Las Margaritas and El Valle, *Woodson et al.* 1293 (F, MO, NY). COLÓN: vicinity of Camp Pina, 25 m, *Allen* 3586 (F, G, NY, U, US); 1 mi. E from Puerto Pilon along road to María Chiquita, *Correa & Haines* 235 (F, MO (2)); vicinity of San Miguel de la Borda, *Croat* 9867 (MO); between Bellas and Salud, near sea level, *Croat* 36870 (MO); along ocean trail between Río Indio and Miquel de la Borda, sea level, *Croat* 36913 (MO); María Chiquita, E of Río Piedras towards Portobelo, *Dwyer & Kirkbride* 7775, 7788 (MO, UC); road to Portobelo between Río Piedras and Portobelo, roadside near ocean, *Elias & Kirkbride* 1648 (MO, UC); without definite locality, *Kuntz s.n.* (NY (2)); Salud, *Lao & Holdridge* 246 (MO); Nuevo Chagres, beach and adjacent roadside, *Lewis et al.* 1856 (MO, US); mouth of Río Piedras, beach and adjacent areas, *Lewis et al.* 3166 (MO, SCZ, UC); coastal thickets between Río Guanche and Río Buenaventura, 7.5 mi. SW of Portobelo, *Webster* 16778 (MO); along roadside between 5–7 mi. SW of Portobelo towards María Chiquita, *Wilbur & Weaver* 11177 (F, MICH, MO, NY, US); 6 mi. SW of Portobelo on the very edge of the Caribbean, *Wilbur & Luteyn* 11665 (DS, F, GH, LL, MICH, MO, NY, US). DARIÉN: coastal thicket near Jaqué, *Duke* 10668 (MO); near Yaviza, 50 m, *Gentry & Mori* 13500 (MO). HERRERA: alrededores de Ocú, *Diaz* 48 (F, MO); road between Las Minas and Pesé, (U. of Fla. site #4), ca. 600 ft., *Duke* 12318 (MO (2)); Ocú, *Ebinger* 1050 (F, MO, US); 10 mi. S of Ocú on Las Minas Road, 300 m, *Graham* 251 (GH, MICH); 12.5 mi. S of Ocú, 1,200 ft., *Lewis et al.* 1633 (ENCB, MO); 1 mi. N of Chupampa on the road to Ocú, *Wilbur et al.* 12108 (DS, F, GH, LL, MICH, MO). LOS SANTOS: 1–2 mi. W of Candelaria, *Duke* 12435 (MO (2)); N of Río Caldera near Punta Mala, *Stimson* 5291 (F, GH, NY, SCZ, UC); Los Asientos, *Wendehake* 37 (MO). PANAMÁ: vicinity of Río Pacora, savannas along Panama National Highway E of Panama City, *Bartlett & Lasser* 16476 (GH, MICH, MO); 1.5 mi. above Interamerican Highway on road to Cerro Campana, *Croat* 12040 (MO); open area near the sea, E side of town, Isla Taboga, *D'Arcy & D'Arcy* 6806 (MO (2), US); Cerro Campana, *D'Arcy* 9600 (MO); near beach at Nueva Gorgona, *Duke* 4514 (MO (2)); Cerro Campana, 2,400–2,700 ft., *Duke* 8674, 10721 (MO); along road from Panamerican Highway to Coronado Beach, *Duke* 11805 (MO); Bar Mouth, Changuinola valley, *Dunlap* 132 (F); Río Mar, near beach, *Dwyer* 1798 (MO); Tocumen, *Dwyer* 1860 (MO); Cerro Campana, ¾ of the way to the summit from Panamerican Highway, *Dwyer et al.* 4849 (MO, SCZ); between Río Pacora and Chepo, roadside savanna, *Dwyer et al.* 5125 (MO, SCZ, UC); La Campana, Cerro Campana, *Ebinger* 370 (F, MO); Playa near Río Mar, *Ebinger* 502 (F, MO); Chagres, *Fendler* 130 (GH, F, US); 1 km E of Chorrera city limits, *Folsom* 3463 (MO); Taboga Island, hill behind beach on main island, near sea level, *Gentry* 5732 (F, MO, NY); Taboga Island, *Killip* 3168 (US); next to bridge over small stream 10.6 mi. W of San Carlos on the Panamerican Highway, *Luteyn & Foster* 1401 (ENCB, F, MO); along the road to Cerro Campana, 600 m, *Miller et al.* 735 (MO); alrededores de Chame, *Moron* 42 (MO); Punta Paitilla, *Piper* 5398 (US); near Old Fort Lorenzo, mouth of Río Chagres, *Piper* 5925, 5932 (US); Las Sabanas, *Standley* 25857 (US); near Punta Paitilla, *Standley* 26282 (US); vicinity of Juan Franco Race Track near Panama, *Stand-*

ley 27795 (US); Taboga Island, *Standley 28021* (US); Tumba Muerto Road, near Panama, *Standley 29785* (US); Nuevo San Francisco, *Standley 30738* (US); dirt road to Ojos de Agua where it branches off the carretera transisthmica (between Panama City and Colón) about 5 mi. N of Panama City, *Stimson et al. 5055* (GH, SCZ, UC); on lower Changuinola River, *Stork 132* (UC, US); Goofy Lake, SW facing slope, 500 m, *Sullivan 78* (MO); W slope of Cerro Campana, 2,300 ft., *Tyson 4038* (MO, SCZ); slopes of Cerro Jefe beyond Cerro Azul between 4–8 mi. in mostly heavily wooded slopes, *Wilbur & Weaver 11345* (DS, GH, MICH, MO); weedy roadsides within 1 mi. of Chepo, *Wilbur & Luteyn 11807* (DS, GH, MICH, MO); Isla Taboga, ca. 0–186 m, *Woodson et al. 1485* (F, MO, NY). SAN BLAS: vicinity of Puerto Obaldía, *Croat 16880* (MO); Isla Soskatupu, *Duke 8945, 10191* (MO); Ailigandi, San Blas Islands, *Dwyer 6809* (MO, TEX); Island of Soskatupu, on the only hill on the island, 150 ft., *Kirkbride 187* (MO, NY); on trail to inland village of Armila, 3–8 km SW of Puerto Obaldía, *Mori et al. 6804* (MO, US). VERAGUAS: ca. 5 mi. N of Santiago, vicinity of Santa María River, *Blum & Tyson 624* (MO, SCZ); 15 mi. W of Santiago, *Croat 10734* (MO); roadside savanna 2–4 mi. E of Santiago, ca. 30 m, *Duke 12366* (MO (2)); Santiago, 12 mi. from Santiago toward divisa on Transisthmian Highway, *Dwyer & Kirkbride 7449* (MO); Santiago, 2 mi. W of Santiago on Transisthmian Highway, *Dwyer et al. 7550* (MO, UC); Río Gatú at intersection with highway from Santiago to Santa Fe, *Folsom 3085* (MO); mouth of Río Concepción, beach, cliffs, and adjacent swamp, *Lewis et al. 2849* (MO, NY, SCZ); road between Laguna La Yeguada and Calobre, *Luteyn 1472* (MO); Proyecto Agro-forestal Alto Guarumo, N of Santiago, S of San Sebastian, 300–400 m, *Meijer & Lao 362* (MO); road to Santa Fe, 15 km from Santiago, 150 m, *Sullivan 409* (MO).

Cordia cymosa (J. D. Smith) Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., 18: 981. 1938. *Cornutia cymosa* J. D. Smith, Bot. Gaz. (Crawfordsville) 40: 10. 1905. TYPE: Costa Rica. Alajuela: Paturages de la Palma, 1,460 m, 19 Nov. 1898, *A. Tonduz 12555* (holotype, US 1323323; isotypes, K, US (2)).

Tree to 15(–30) m tall, the twigs ferruginous-tomentulose with scattered echinate hairs. Leaves persistent; petioles 15–41 mm long, shallowly canaliculate adaxially, ferruginous-tomentulose with scattered echinate hairs; blades dimorphic, the larger ones elliptic or elliptic-ovate, (15–)18–32(–37.5) cm long, (7.5–)11–20.5(–26) cm wide, the smaller ones orbicular to circular, 9.5–16 cm long, 8.5–17 cm wide, the apex obtuse or less commonly rounded or acute, the base obtuse or less commonly acute, the margin

entire, the adaxial surface strigillose, the abaxial surface soft-pubescent, with most of the the hairs restricted to the veins. Inflorescence terminal, cymose, (14.5–)17–29 cm long, 18.5–31 cm broad, the peduncle (1–)3.5–8.2(–11.2) cm long, ferruginous-tomentulose with scattered echinate hairs. Flowers sessile, unisexual by abortion, the plants dioecious, the male flowers with reduced styles, the female flowers with small, nonfunctional anthers. Female flowers with a tubular calyx ca. 3.7 mm long; corolla white, tubular with reflexed lobes, 4.6–5.3 mm long, 5-merous, the lobes oblong-ovate, 2–2.2 mm long, 1–1.2 mm wide, the tube 2.4–3.3 mm long; stamens 5, nonfunctional, the filaments ca. 3.5 mm long, the upper 0.5–1.8 mm free, glabrous or nearly so, the anthers ellipsoid, shriveled, 0.2–0.4 mm long; ovary ellipsoid to ovoid, 1.5 mm long, 0.8–0.9 mm broad, glabrous; disc small, crateriform or indistinct from the base of the ovary; style 2.5–3.5 mm long, the stylar branches 1.2–2 mm long, the stigma lobes clavate to discoid. Male flowers with a campanulate calyx, 2.2–3 mm long, 2–3 mm wide at mouth, strigillose to puberulent, the 3–5 lobes depressed-ovate to deltate, ca. 0.8 mm long; corolla white, tubular-campanulate with reflexed lobes, 3.8–4.7 mm long, the 5 lobes oblong-ovate, 1.9–2.1 mm long, 1–1.4 mm wide, the tube 2–2.7(–3.8) mm long; stamens 5, the filaments (2.5–)4–5 mm long, the upper 1.6–2.4 mm free, pubescent at and just above the point of insertion, the anthers ellipsoid to oblong, 0.8–1 mm long; ovary ovoid, 0.6–1 mm long, 0.4–0.6 mm broad, glabrous; disc crateriform, 0.3–1 mm tall, 0.6–1.2 mm broad, or occasionally not distinct from the base of the ovary, glabrous; style 0.7–1(–1.8) mm long, the stylar branches 0.3–0.5(–1) mm long, the stigma lobes filiform to clavate. Fruits seated in the cupulate calyx, white, drupaceous, glabrous, the stone inequilaterally ovoid, 7.3–10 mm long, 4.8–9 mm broad, endocarp bony, 1-locular.

Distribution. *Cordia cymosa* ranges from Costa Rica south through Panama and

Colombia to Ecuador, mostly in cloud forests and rarely at low elevations in wet forests. In Panama it is known from Bocas del Toro, Canal Area, Coclé, and Panamá.

Cordia cymosa is a member of the *C. panamensis* group, one of the taxonomically most complex species groups of sect. *Myxa*. It is probably most closely related to *C. panamensis* but differs by having larger stature. *Cordia cymosa* is easily distinguished from the other members of the complex by its scattered echinate hairs on the stems, petioles, and peduncles.

Additional specimens examined. PANAMA. CANAL AREA: Mt. Lerio, *Christopherson 152* (US (2)). BOCAS DEL TORO: region of Cerro Colorado, 4.3 mi. above Camp Chami, 1,500 m, *McPherson 9595* (MO). COCLÉ: El Valle de Antón, *Alston 8809* (US). PANAMÁ: Cerro Campana, *Folsom et al. 2312* (MO); Cerro Campana, trails just inside entrance to Parque Nacional, 850 m, *Miller & Miller 998* (MO); along the Panamerican Highway 6.5 mi. E of highway checkpoint at turnoff to Chepo, *Miller et al. 1018* (MO).

***Cordia dentata* Poiret, Encycl. 7: 48. 1806.**

TYPE: Curasao: *Von Rohr 1799* (holotype, P in herb. Jussieu, not seen; microfiche, MO).

Cordia calyptrata Bertero ex Sprengel, Syst. Veg. 1: 649. 1825. *Varronia calyptrata* (Bertero ex Sprengel) DC., Prodr. 9: 469. 1845. TYPE: Mexico, Veracruz: near Vera Cruz, 1,000 ft., 1839, *J. J. Linden 284* (holotype, BR; isotypes, K, MICH).

Cordia tenuifolia Bertol., Rendiconto Sess. Ordinarie Accad. Sci. Ist. Bologna 1860–1861: 63. 1860; Mem. Reale Accad. Sci. Ist. Bologna, 11: 199, t. 11. 1861. TYPE: Guatemala: In Volcano d'acqua a Vallesquezio (not seen).

Cordia leptopoda K. Krause, Bot. Jahrb. Syst. 37: 628. 1906. TYPE: Colombia: in planitiebus ad flumen Magdalena, prope Purificacion, 200–500 m, *Lehmann 7347* (not seen).

Cordia ovata Brandegee, Univ. Calif. Publ. Bot. 10: 187. 1922. TYPE: Mexico. Veracruz: Remudadero, *C. A. Purpus 8937* (holotype, UC; isotypes, GH, MO, NY, US).

Tall shrub or tree to 7(–10) m tall, the twigs puberulent to nearly glabrous. Leaves semideciduous; petioles 8–20 mm long; blades elliptic to widely elliptic or ovate, occasionally obovate, 4.6–10 cm long, 3–7 cm wide, the apex obtuse, or less commonly acute or rounded, the base obtuse to rounded, rarely acute, the margin entire or slightly denticu-

late, the adaxial surface strigillose to scabrous, the hairs arising from a distinct cystolith, the abaxial surface nearly glabrous to puberulent with dense tufts of curly hairs in the axils of the major veins. Inflorescence terminal, cymose-paniculate, 15–20 cm broad, the branches puberulent to sparsely strigillose. Flowers sessile, distylous; calyx campanulate, 3–3.8 mm long, circumscissile and tearing open somewhat unevenly, faintly 10(–12)-ribbed; corolla yellow to almost white, campanulate, 9–12 mm long, 5(–6)-merous, the lobes depressed ovate, 1.8–4 mm long; stamens 5(–6), the filaments 4.7–9.4 mm long, puberulent at the point of insertion, the anthers ellipsoid to oblong, 1.2–2 mm long; ovary ellipsoid to globose, 1–1.5 mm long; style 3.5–5.3 mm long, the stigma lobes clavate. Fruits borne in the saucer-shaped calyx, translucent white, drupaceous, the stone ellipsoid, symmetrical or nearly so, 9–11 mm long, 5.5–7.2 mm broad, the endocarp bony.

Distribution. *Cordia dentata* occurs in dry forests from sea level to 400(–1,400) m in elevation from Mexico to northern South America and the West Indies. In Panama this species is known from the Canal Area and the provinces of Chiriquí, Herrera, Los Santos, Panamá, and Veraguas.

Cordia dentata is the most distinctive member of sect. *Myxa* in Central America. It is the only species with a yellow corolla that is relatively large, campanulate, and rather showy, and it is often cultivated for this reason, as well as for its sweet, edible fruits. It differs further from most other members of the section by having a circumscissile calyx. The unusual calyx and corolla of *C. dentata* suggest that it is not closely related to any of the other Panamanian members of sect. *Myxa*, and its relationships with species from other geographic regions are obscure. Johnston (1940) stated that the type of *C. dentata* was collected by Von Rohr, but the only sheet in the Jussieu herbarium is labeled as a Vahl collection. It was apparently collected by Von Rohr, and the sheet at Paris is a duplicate that Poiret received from Vahl.

Cordia dentata is common throughout

much of Mexico, Central America, the West Indies, and northern South America but has been only rarely collected in Panama. While most species of sect. *Myxa* occur in wet forests, *C. dentata* occurs in drier regions, often in second-growth and disturbed areas. It is frequently found growing along roadside ditches and fencerows from Costa Rica northward.

Additional specimens examined. PANAMA. CANAL AREA: Monte Lirio, *Christopherson 125* (US); between Gorgona and Mamei, 10–30 m, *Pittier 2236* (NY, US). CHIRIQUÍ: vicinity of David, *Pittier 2820* (GH, NY, US); vicinity of San Felix, 0–120 m, *Pittier 5448* (GH, NY), *5458* (US). HERRERA: Pesé, ca. 20 m, *Allen 805* (MO, NY (2), US); Chitré, *Carrasquilla 314* (F, MO); ca. 2 mi. E of Chitré, *D'Arcy & Croat 4190* (MO, SCZ); outskirts of Chitré, *D'Arcy & Antonio 13481* (MO); Las Minas, 350 m, *Lao 45* (MO). LOS SANTOS: Las Tablas, *Dwyer 1167* (MO (2)); Monagre Beach, *Dwyer 4165* (MO); road from Macaracas to Chitré Highway, *Tyson et al. 3156* (MO, SCZ). PANAMÁ: near Chepo, *Kluge 52* (CFMR, F, US). VERAGUAS: 5 mi. E of Santiago, *Tyson et al. 4289* (MO, SCZ).

Cordia diversifolia Pavón ex A. DC. in DC., *Prodr.* 9: 474. 1845. TYPE: Nueva España, *Pavón s.n.* (holotype, G-DC, not seen; microfiche, MO; isotype, G).

Cordia johnstonii Cuf., *Arch. Bot. Sist.* 10: 41. 1934. TYPE: Costa Rica. Atlantida: 28 mi. from Puerto Limón, *Cufodontis 365* (not seen).

Cordia petenensis Lundell, *Wrightia* 4: 49. 1968. TYPE: Guatemala. Petén: Remate, 26 Apr. 1960, *E. Contreras 894* (holotype, LL; isotypes, F, K).

Shrub to slender tree to 5(–10) m tall, the twigs hispid to hirsute. Leaves persistent; petioles 5–19 mm long, hispid to hirsute; blades narrowly elliptic or sometimes lanceolate or oblanceolate, 10.5–19 cm long, 3.2–6.8 cm wide, the apex acuminate to acute, the base acute, the margin with few, short, filiform teeth toward the apex or entire, the adaxial surface strigose, the abaxial surface soft strigose, the hairs mostly restricted to the veins. Inflorescence terminal, paniculate, 5.5–11 cm broad, the branches hispid to villous. Flowers sessile or on short spurs to 2(–4) mm long, unisexual by abortion, the plants dioecious, the male flowers lacking styles, the female flowers with small, nonfunctional anthers; calyx tubular, 4.5–5.5 mm long, 10-ribbed, 3–4(–5)-lobed; corolla white, tubular with re-

flexed lobes, 8–9.5 mm long, 5-merous, the lobes oblong to obovate; stamens 5, in male flowers the filaments 7.7–9(–10.7) mm long, the upper (3–)4.5–5.3 mm free, glabrous or the lower free portion pubescent, the anthers oblong, 0.4–1.8 mm long, in female flowers the stamens much reduced, the anthers 0.4–0.7 mm long; ovary ovoid, 0.4–1.2 mm long; disc widely depressed obovoid, 0.5–1 mm tall, style 7–8.5 mm long, absent in male flowers, the stigma lobes filiform. Fruits borne in the expanded, saucer-shaped calyx, white, drupaceous, the stone ovoid to ellipsoid, 7–9 mm long, 4–6 mm broad, the endocarp bony.

Distribution. *Cordia diversifolia* occurs in wet forests of the Atlantic coast from sea level to 600 m in elevation from Mexico to Panama. In Panama this species is known from Bocas del Toro and the Canal Area.

Cordia diversifolia is an uncommon species of Atlantic lowland forests in Central America but is apparently quite common in lowland Bocas del Toro. It is distinctive in its narrowly elliptic to lanceolate leaves, leaf margins with short, filiform teeth, costate calyx, and filiform stigma lobes. This is the most widespread member of a small complex of closely related Central American species that is defined by the presence of denticulate leaf margins, costate calyces, and consistent dioecy. The group also includes *C. cordiformis* I. M. Johnston, *C. salvadorensis* Standley, and *C. skutchii* I. M. Johnston, all of which occur from Nicaragua northward.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Almirante, out along the road to the “Bomba,” *Blum 1314* (MO, SCZ); Lincoln Creek, *Carleton 40* (NY, US); Changuinola Valley, *Cooper & Slater 61* (CFMR, F), *112* (CFMR, F, US); region of Almirante, *Cooper 342* (CFMR, F (2), NY, US); Changuinola, *Croat 16309* (F, MO, NY); Changuinola Valley, *Dunlop 175* (F, US); Changuinola to 5 mi. S at junction of ríos Changuinola and Terebe, 100–200 ft., *Lewis et al. 795* (MO, UC, US), *937* (K, MO, US), *938A* (MO), *946* (F, MO, NY, UC, US); Chiriquí to 5 mi. S along Río Guarumo, *Lewis et al. 1994* (F, MO (2), US); Almirante, near road to Chiriquí, *McDaniel 5077* (MO); Shepherd Island, *McDaniel 5077, 5161* (MO); on lower Changuinola River, *Stork 284* (UC, US); Almirante region, *Taylor & Slater 61* (US); Chiriquí Lagoon, Water Valley, *Wedel 632* (MO); Chiriquí Lagoon, *Wedel 1070* (MO); Chiriquí Lagoon, Old Bank Island, *Wedel 1894* (GH, MO, US), *2051* (MO, US); Chiriquí Lagoon, Pumpkin River, *Wedel*

2580 (MO, US); Chiriquí Lagoon, *Wedel* 2595 (MO, US); vicinity of Nievécita, ca. 0–50 m, *Woodson et al.* 1824 (F, MO, NY); Río Cricamola, between Finca St. Louis and Konkintoe, ca. 10–50 m, *Woodson et al.* 1895 (MO, NY). CANAL AREA: Gamboa Naval Reservation, *Ebinger* 482 (BR, ENCB, F, GH, MO).

Cordia dwyeri Nowicke, *Phytologia* 18: 419. 1969. TYPE: Panama. Colón: Santa Rita Ridge, 19 km from the Transisthmian Highway, 28 Jan. 1968, *J. D. Dwyer* 8857 (holotype, MO 2518567; isotypes, F, GH, MO).

Sparsely branched tree to 10(–20) m tall, the twigs reddish-brown villous. Leaves persistent; petioles (2–)4–8(–14) mm long, thick, villous; blades coriaceous, bullate, ovate to elliptic, (9–)19–35(–60) cm long, (5–)8–16(–25) cm wide, the apex acuminate to acute, the base rounded to obtuse or rarely subcordate, the margin entire, revolute, the adaxial surface distinctly bullate, often drying with a silver cast, nearly glabrous with a few scattered, appressed hairs, the abaxial surface brown pubescent to densely brown pilose. Inflorescence axillary or terminal, cymose, 4–15(–23) cm broad, the branches densely velutinous to tomentose, the hairs reddish brown. Flowers sessile, bisexual, monomorphic; calyx cupulate, 6–7 mm long, ribs absent, densely strigillose, with 2–3 unevenly deltate lobes; corolla white, cupulate with reflexed lobes, 8–9.5(–10.6) mm long, 5-merous, the lobes ovate to widely elliptic, 3–4 mm long, the tube 4.5–7 mm long; stamens 5, the filaments (5–)8–11(–13) mm long, the upper (2–)4.5–6.5 mm free, densely pubescent just above the point of insertion, the anthers ellipsoid to oblong, 1.4–1.8 mm long; ovary ovoid to conical, 1–1.7 mm long, glabrous; disc transversely oblong, 0.4–0.8 mm long; style 5–7.4 mm long, the stigma lobes clavate. Fruits half enclosed in the slightly accrescent calyx, white, drupaceous, inequilaterally ovoid, the stone ca. 1.7 cm long, ca. 1.3 cm broad, the endocarp bony, pebbled on the surface.

Distribution. *Cordia dwyeri* occurs in wet forests from sea level to 450 m in elevation and ranges from southern Nicaragua

to northern South America. In Panama this species is known from the provinces of Bocas del Toro, Colón, and Panamá.

Cordia dwyeri appears to have no close relatives in Central America and is very distinctive in its habit of growth and in its extremely large, bullate leaves. Its closest relative is probably *C. trichoclada* DC. of South America, a species that has large bullate leaves but differs in having a costate calyx. *Cordia dwyeri* is apparently common throughout lowland wet forests of Costa Rica and Panama, although it is not often collected. This may be due to relatively rare flowering or may relate to the difficulty of preparing specimens from such bulky plants.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Palo Blanco, *Gordon* 95c (MO). COLÓN: East Santa Rita Ridge, *Correa & Dressler* 663 (MEXU, MO); Santa Rita Ridge, *Croat* 13856 (MO). PANAMÁ: El Llano–Carti Highway, about 8 km N of El Llano, *Dressler* 4573 (ENCB, F, MO); forest and roadside between 6–12 km N of El Llano on Carti Road, 1,200 ft., *Hammel* 866 (MO); El Llano–Carti Road, 7.9 km from Interamerican Highway, 400 m, *Miller et al.* 872 (MO); El Llano–Carti Road, 7.9 km from Interamerican Highway, 350 m, *Mori & Kallunki* 5608 (AAU, MO, NY); along El Llano–Carti Road, 7 km N of Pan-American Highway at El Llano, 450 m, *Nee* 10402 (MEXU, MO, US); El Llano–Carti Road, ca. 9 mi. from Pan-American Highway along newly cut bypass, 350–400 m, *Sytsma* 4145 (MO).

Cordia eriostigma Pittier, *Contr. U.S. Natl. Herb.* 18: 251, fig. 101. 1917. TYPE: Colombia. Cauca: El Paso de la Balsa, on the Cauca River, near Jamundi, 480 m, 10 Feb. 1906, *H. Pittier* 1489 (holotype, US 531695).

Tree to 15(–30) m tall, the twigs minutely brown strigillose, later waxy. Leaves persistent; petioles (7–)10–24(–30) mm long, sparsely strigillose; blade elliptic or slightly ovate or obovate, occasionally narrowly elliptic, (5–)6–16(–22.5) cm long, (2.4–)4.3–7.5(–11) cm wide, the apex usually obtuse and acuminate at the very tip, occasionally acute or rounded, the base obtuse to acute, the margin entire, the adaxial surface glabrous or nearly so, usually with small papillae, the abaxial surface with few, small, scattered hairs, some attached medianly. Inflorescence

terminal, cymose, 8–13(–17) cm broad, the branches brown strigillose. Flowers sessile, bisexual, monomorphic; calyx cupulate to campanulate, 2.8–3.5(–4.7) mm long, ribs absent, evenly strigillose, opening without distinct lobes or unevenly 3–5-lobed; corolla white, campanulate, 5.7–6.3(–7.3) mm long, 5(–6)-merous, the lobes deltate to shallowly deltate, (2.5–)3–4.3 mm long, the tube 2.4–3.4 mm long; stamens 5(–6), the filaments (4–)5–5.5 mm long, the upper (1.4–)2–2.5 (–3) mm free, puberulent below insertion, the hairs often spreading onto corolla tube; anthers oblong to ellipsoid, 1–1.7 mm long; ovary ovoid to broadly ovoid, 1.3–2 mm long, glabrous or with short bristles on the upper portion; disc crateriform, small; style 1.5–2.6 mm long, the stigma lobes spatulate to discoid. Fruit borne in the saucer-shaped calyx, red to orange at maturity, drupaceous, glabrous, the stone inequilaterally ovoid, 6–7 mm long, 3.5–5.5(–6) mm broad, the endocarp bony.

Distribution. *Cordia eriostigma* occurs in moist to wet forests at 200–1,200 m in elevation and ranges from Mexico to Colombia. In Panama this species is known only from the province of Coclé.

Cordia eriostigma is uncommon and is often confused with *C. collococca*, from which it can be distinguished by having persistent leaves with nearly glabrous abaxial surfaces, bisexual flowers, campanulate corollas, valvate calyx lobes, and ovaries with distinct bristles on the upper portion. *Cordia eriostigma* differs further from *C. collococca* in usually being found above 600 m in elevation.

Additional specimens examined. PANAMA, COCLÉ: El Valle site area of WEPCOR, Cerro Pilón, *Kirkbride 1071* (MO, US); El Valle de Antón, *Lao 281* (F, MO).

Cordia globosa (Jacq.) Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 76. 1818; *Varronia globosa* Jacq., Enum. Syst. Pl. 14. 1760. TYPE: not seen.

Varronia humilus Jacq., Enum. Syst. Pl. 14. 1760. *Cordia humilus* (Jacq.) D. Don, Gen. Hist. 4: 383. 1838. *Cordia globosa* var. *humilus* (Jacq.) I. M.

Johnston, J. Arnold Arbor. 30: 98. 1949. TYPE: not seen.

Cordia jacmeliana K. Krause, Bot. Centralbl. 32: 344. 1914. *Varronia jacmeliana* (K. Krause) Friesen, Bull. Soc. Bot. Genève, Ser. 2, 24: 177. 1933. TYPE: Haiti. Ouest: near Jacmel, *Krause 11808* (not seen).

Varronia humilus var. *mexicana* Friesen, Bull. Soc. Bot. Genève, Ser. 2, 24: 162, t. 1, f. 4. 1933. *Varronia mexicana* Friesen, Bull. Soc. Bot. Genève, Ser. 2, 24: 162. 1933. TYPE: Mexico. Morelos: near Cuernavaca, 5,000 ft., 22 June 1896, *C. G. Pringle 6346* (holotype, G; isotypes, BR, CAS, ENCB, F, K, L, LE, MEXU (2), MO, NY, US (3)).

Shrub to 3(–4) m tall, the twigs strigillose. Leaves deciduous, on short spurs to 1 mm long; petioles (2–)3–12(–25) mm long, strigillose, the hairs appressed to spreading; blades ovate to lance-ovate, (1.3–)2–5.7(–9) cm long, (0.7–)1–2.7(–5) cm wide, the apex acute, the base subobtuse to acute and decurrent along the petiole for a short distance, the margin serrate, usually unevenly so, the teeth usually blunt, occasionally short-apiculate, the adaxial surface usually \pm smooth, occasionally slightly bullate, strigose to strigillose, or scabrous, the abaxial surface strigillose to strigose, most of the hairs restricted to the veins, rarely nearly tomentose. Inflorescence subterminal, a dense, globose head, 8–14(–16) mm broad, the peduncle 0.5–1.5 (–3.6) cm long, strigillose. Flowers sessile, distylous; calyx campanulate, (2.3–)3–4(–4.2) mm long, ribs absent, the 5 lobes deltate to triangular with prolonged filiform tips 2–4 mm long; corolla white, tubular, (5–)6–8 (–10) mm long, undulate to shallowly lobed, the lobes scarcely separate to transversely elliptic-oblong, the tube (2.4–)3–4(–4.5) mm long; stamens 5, the filaments (4.5–)5–8(–9) mm long, the upper (1.3–)2–3(–4) mm free, puberulent in a ring in the mouth of the corolla tube, the anthers ellipsoid, 0.8–1.1 mm long; ovary ovoid, 1–1.5(–1.8) mm long; disc crateriform, 0.5–1 mm tall; style (3–)4.5–7 (–7.5) mm long, the stigma lobes filiform to clavate. Fruits drupaceous, red, the stone ovoid, 3.5–4.8 mm long, (1.5–)2–3.8 mm broad, the endocarp bony.

Distribution. *Cordia globosa* occurs in dry to moist forests from sea level to 600 m

in elevation and ranges from southern Florida and Mexico to northern South America and the West Indies. This species is known in Panama from one collection.

Cordia globosa is a common weedy shrub throughout Central America, the West Indies, and parts of northern South America, but apparently rare in Panama. *Cordia globosa* is most closely related to *C. bullata*, which ranges from Costa Rica to Mexico and the West Indies, but the former differs in having corollas more than 5 mm long and peduncles less than 3.6 cm long. The leaves of *C. globosa* are also generally smaller and have a less prominent indument. Nevertheless, these two species are often difficult to separate, and interspecific hybridization appears to occur in some populations in Nicaragua, Honduras, and Yucatán (Miller, in prep.).

Jacquin did not specify a type when he published the names *Varronia globosa* and *V. humilus*. None of his collections of this species seem to be present in the Willdenow or Linnaean herbaria. There may be a specimen at BM (Stafleu, 1967), but Johnston (1949c) stated that no type was preserved. Proper lectotypification will have to await examination of specimens in European herbaria. An odd situation exists with *Varronia humilus* var. *mexicana* and *Varronia mexicana*, two names published by Friesen based on the same type for either a new species or a new variety. Friesen did not indicate at which rank he felt it should be treated.

Additional specimens examined. PANAMA. PANAMÁ: Punta Paitilla, Standley 26268 (US).

Cordia inermis (Miller) I. M. Johnston, J. Arnold Arbor. 30: 95. 1949. *Lantana inerma* Miller, Gard. Dict. ed. 8, 1768. TYPE: Mexico. Veracruz: Houston s.n. (holotype, BM, not seen).

Cordia cana Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 11: 331. 1844. TYPE: Mexico. Oaxaca: Bois de la late Pacifique, 1840, Galeotti 7140 (holotype, BR).

Cordia insularis Greenman, Proc. Amer. Acad. Arts 33: 482. 1898. TYPE: Mexico. Nayarit: Tres María Islands, 3–25 May 1897, E. W. Nelson 4296 (holotype, GH; isotype, US).

Erect shrub to 2(–3) m tall, the twigs strigillose to puberulent when young, later glabrous and lenticellate. Leaves deciduous; petioles (2–)4–12(–22) mm long, strigillose to puberulent; blades elliptic-ovate to narrowly elliptic or elliptic-lanceolate, (2–)3.5–10(–14) cm long, (0.7–)1–3.5(–6.8) cm wide, the apex acuminate to acute, the base attenuate, the margin serrate, the adaxial surface strigillose to strigose, the abaxial surface strigillose. Inflorescence internodal or terminal, a small globose head, (3–)4–7(–10) mm broad, the peduncle (0.7–)1–5(–9) cm long, strigillose to puberulent. Flowers sessile, appearing unisexual, the plants subdioecious, the male flowers with reduced styles, the female flowers smaller than the males, with small nonfunctional anthers; calyx campanulate, 1.8–3 mm long, ribs absent, strigillose, the (4–)5 lobes deltate, 0.5–1 mm long; corolla white to greenish white, 2.5–3.5(–3.8) mm long, truncate to undulate but lacking distinct lobes, puberulent to pubescent in the middle of the tube; stamens 4–5, in male flowers the filaments (3.3–)3.5–4 mm long, the upper 1–1.6 mm free, puberulent at insertion, the anthers oblong, 0.7–1 mm long, in female flowers the filaments 2–2.5 mm long, the upper 0.3–0.5 mm free, puberulent at insertion, the anthers ellipsoid, ca. 0.3 mm long; ovary ovoid to nearly spherical, 0.5–1 mm long; disc crateriform, 0.2–0.6 mm tall; style in male flowers 0.7–1 mm long, the stigma lobes much reduced, filiform to slightly flattened, the style in female flowers 2–3.5 mm long. Fruits drupaceous, (3–)4–5.5(–6.5) mm long, 2–3(–3.2) mm broad, $\frac{1}{3}$ – $\frac{2}{3}$ enclosed in the slightly accrescent calyx, the calyx and fruit bright red at maturity, the stone ovoid, the endocarp bony.

Distribution. *Cordia inermis* occurs in disturbed areas from sea level to 1,100 m in elevation and ranges from Mexico to Panama. In Panama this species is known from the Canal Area, Chiriquí, and Panamá.

Cordia inermis is one of the most common weedy species of the genus in Central America. It reaches its southern limit in Panama

where it is known from relatively few collections. In Panama, *C. inermis* can be confused with *C. linnaei*, from which it differs in having terminal or internodal rather than axillary inflorescences.

Cordia inermis has been described as dioecious (Opler et al., 1975). The female flowers have small nonfunctional anthers, and the male flowers have reduced styles and stigmas. The pollen from anthers of female flowers is small, deformed, and completely nonstainable. The female flowers appear to be 100% male sterile, but there is no indication of complete female sterility in male flowers, even though the gynoecium is reduced. In fact, some collections of male plants have both flowers and fruits on the same branch, and this species is probably subdioecious.

Additional specimens examined. PANAMA. CANAL AREA: Quarry Heights, hilltop, *Dwyer 2610* (MO (2), NY, US). CHIRIQUÍ: 1 mi. W of airport at Puerto Armuelles, near sea level, *Croat 22531* (F, MO); Río San Cristobal, 2 mi. W of David, 150 ft., *Tyson 912* (MO, RSA). PANAMÁ: Taboga Island, *Standley 27039* (US); *Woodson et al. 1478* (F, MO, NY).

Cordia lasiocalyx Pittier, Contr. U.S. Natl. Herb. 18: 251. 1917. TYPE: Panama. Darién: open field around Garachine, sea level, 12 Feb. 1912, *H. Pittier 5694* (holotype, US 715984; isotype, F).

Shrub or small tree to 5(-10) m tall, the branching pattern divaricate, the twigs glabrous. Leaves persistent; petioles (3-)4-7 (-10) mm long, canaliculate adaxially, glabrous; leaf blades elliptic-oblong to slightly obovate, (6-)9-13(-16) cm long, (2-)2.6-5(-5.4) cm wide, the apex abruptly caudate, the caudex (1-)2-3(-3.5) cm long, the base acute and slightly decurrent, the margin entire, the adaxial surface glabrous, the abaxial surface sparsely and minutely strigillose. Inflorescence terminal, cymose, 2.5-6.5(-10) cm broad, the peduncle 2.5-5 cm long, glabrous or with a few widely scattered hairs. Flowers sessile, monomorphic, the stamens exceeding the style; calyx cupulate to campanulate, 3.8-5 mm long, 3.6-4 mm wide at the mouth, ribs absent, glabrous or nearly so, the 3 lobes deltate, 1-2 mm long; corolla

white, tubular, 7.6-10 mm long, 5-merous, the lobes oblong, 3.3-4.6 mm long, 2-2.5 mm wide, the tube 4.3-6 mm long; stamens 5, the filaments 6-9.5 mm long, the upper 2.6-3 mm free, pubescent at insertion, the anthers oblong, ca. 1.3 mm long; ovary ovoid to broadly ovoid, 1.3-1.8 mm broad, glabrous; style 3.5-5 mm long, the stylar branches 1.6-2.2 mm long, the stigma lobes clavate. Fruits borne in the cup-shaped calyx, white, drupaceous, glabrous, the stone strongly inequilaterally ovoid, 10-11 mm long, 6.4-9 mm broad, ruminant, the mesocarp mucilaginous, endocarp bony, 1-locular.

Distribution. *Cordia lasiocalyx* occurs in moist forests from sea level to 800 m in elevation and is known only from Panama, where it occurs in Bocas del Toro, the Canal Area, Coclé, Darién, and Panamá.

Cordia lasiocalyx is a member of a taxonomically difficult species complex that is characterized by glabrous leaves, a three-lobed calyx, and white fruit. Its caudate leaf apex readily separates it from its closest Central American relatives, *C. croatii*, *C. lucidula*, and *C. porcata*, all of which have acuminate leaf apices. *Cordia lasiocalyx* is probably most closely related to *C. lomatiloba* I. M. Johnston, a species of Amazonian South America.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Island Potrero, Changuinola Valley, *Dunlap 322* (F, GH, US). CANAL AREA: Barro Colorado Island, *Croat 4601* (F, NY, SCZ (2)), 8568, 8572 (DUKE, F, MO, NY, SCZ); *Foster 833* (DUKE); *Knight 69-20* (MO (2)); *Oppenheimer 837* (DUKE, MEXU, MO, TEX); *Shattuck 813* (F, MO (3)), 853 (F, MO (2), US). COCLÉ: El Valle de Antón, *Allen 2302* (MO); Cerro Pilón, 2,500-3,000 ft., *Dwyer 8315* (DUKE); along ridge of Cerro Gaital, N slope of mountains near La Mesa, N of El Valle, 800-900 m, *Knapp & Dressler 4879* (MO); La Mesa, 2 km W of Cerro Pilón, 860 m, *Sullivan 453, 498* (MO). DARIÉN: Río Pirre, *Duke & Bristan 8282, 8300* (MO); Puerto Indio, less than 50 m, *Hammel 1080* (MO); Trail from Canglon-Yaviza Road to Río Chucanaque, 7.7 mi. E of Canglon, 50 m, *Knapp & Mallet 3956* (MO); forests around Pinogana, *Pittier 6560* (US). PANAMÁ: Río Maje, along river from waterfalls near Bayano Lake to finca of Choco Indian Eduardo Maycha, ca. 2 mi. upstream, 30-60 m, *Croat 34581* (MO); vicinity of El Llano, *Duke 5837* (MO); del G.M.I. Isla Bayano, *Garibaldi 97* (F, MEXU, MO); Cerro Campana, 900 m, *Knapp & Sytsma 2308* (MO); Cerro Campana, above Su Lin Motel, *Porter et al. 4218* (MO).

Cordia leslieae James S. Miller, sp. nov.

TYPE: Panama. Panamá: Cerro Jefe 5.8 mi. above Lago Cerro Azul, 840 m, 30 July 1983, *James S. Miller & Leslie A. Miller 886* (holotype, MO 3386970). Figure 4.

Arbor ad 7 m alta, ramunculis glabris, subalatis. Folia persistentia, petiolis 0.8–2 cm longis, applanatis, basibus continuis secus ramos; lamina coriacea, obovata, 9.2–16.2 cm longa, 5.3–8.4 cm lata, apicibus retusis ad acuminatis, basibus cuneatis, marginibus integris, revolutis. Inflorescentia terminalis, cymo-paniculata. Flores bisexualis; calyx tubulo-campanulatus, 5.5–6 mm longus; corolla alba, 8–10 mm longa, 5-lobata, lobis ovatis, incrassatis ad apices, stamina 5. Fructus drupaceus, aurantiacus, putamine inaequaliter ovoideo, 1.4 cm longo.

Tree to 7 m tall, the twigs glabrous, subalate. Leaves persistent; petioles 0.8–2 cm long, flattened in cross section and canaliculate adaxially, the bases continuous along the stem for a short distance; blades coriaceous, obovate, 9.2–16.2 cm long, 5.3–8.4 cm wide, the apex variable, retuse or acuminate, the base cuneate, the margin entire, revolute, the adaxial surface glabrous, slightly papillose, the abaxial surface glabrous. Inflorescence terminal, cymose-paniculate, 5.5–7.5 cm long, 5–9.5 cm broad, with 50–120 or more flowers, the branches sparsely strigillose. Flowers sessile or nearly so, bisexual; calyx tubular-campanulate, 5.5–6 mm long, 3–3.4 mm wide at the mouth, ribs absent, sparsely strigillose, the 5 lobes deltate, 1–1.4 mm long; corolla white, tubular with reflexed lobes, 8–10 mm long, 5-merous, the lobes ovate to oblong with a triangular thickening at the apex, 4 mm long, 2–3 mm wide, the tube 4–6 mm long; stamens 5, the filaments 9.3 mm long, the upper 4.3 mm free, pubescent at insertion, the anthers oblong, 2 mm long; ovary obloid, 1.8 mm long, 0.7 mm broad; style 5.5 mm long, the stylar branches 2 mm long, the stigma lobes clavate to discoid. Fruits seated in the cupulate, slightly accrescent calyx, orange, drupaceous, the stone inequilaterally ovoid, 1.4 cm long, mesocarp mucilaginous, endocarp bony, 1-locular.

Distribution. *Cordia leslieae* occurs in cloud forests at 800–1,000 m in elevation

and is known only from Cerro Jefe, in the province of Panamá.

Cordia leslieae is apparently not closely related to any other species of *Cordia* in Central America. This species is distinct in having sub-alate stems and petioles and in having thickened areas at the ends of the corolla lobes. It is named in honor of my wife, Leslie Miller, who assisted me with field studies in Panama and discovered the tree from which the type collection was made.

Additional specimens examined. PANAMA. PANAMÁ: Cerro Jefe, *Dressler 3489* (MO, PMA); Cerro Jefe region roadside and forest, 200–800 m, *Hammel 4850* (MO); Cerro Jefe, NE of Panama City, forested slopes below summit, 850–900 m, *McPherson 9735* (MO); Cerro Jefe, near summit, along road to east about a quarter mile below tower, 750–850 m, *McPherson 11191* (MO); Cerro Jefe, 850–900 m, *Sytsma 2009* (MO).

Cordia linnaei Stearn, *J. Arnold Arbor.* 52: 627. 1971. TYPE: Jamaica. St. Andrews: pastures behind Hope Gardens, 600–700 ft., 22 Oct. 1956, *Proctor 15789* (holotype, BM, not seen; isotype, IJ).

Shrub to 4 m tall, the twigs coarsely pubescent, the hairs erect, brown. Leaves deciduous, on short spurs 1–1.5 mm long; petioles (1–)1.5–3(–7) mm long, pubescent, the hairs erect, brown; blades ovate to lanceolate, (2–)3.4–9(–10.6) cm long, (0.9–)1.2–2.9(–5.3) cm wide, the apex acute to acuminate, the base cuneate, the margin sharply serrate, the adaxial surface coarsely puberulent, the hairs short, slightly swollen at the base, appressed, the abaxial surface softly pubescent, the hairs wavy, erect. Inflorescences numerous, axillary, capitate, 7–11 mm broad, the peduncle (0.5–)0.8–2.8(–6.4) cm long, pubescent, the hairs erect, brown. Flowers sessile, distylous; calyx cup-shaped, 2–2.5(–2.7) mm long, ribs absent, strigillose, the 5(–6) lobes deltate to shallowly triangular, sometimes with a short apiculate tip; corolla white, tubular, 3–3.8(–4.2) mm long, truncate at the apex; stamens 5, the filaments (2.5–)3–3.5(–3.8) mm long, the upper 0.3–1(–1.2) mm free, glabrous to canescent at insertion, the anthers ellipsoid, 0.4–0.6 mm

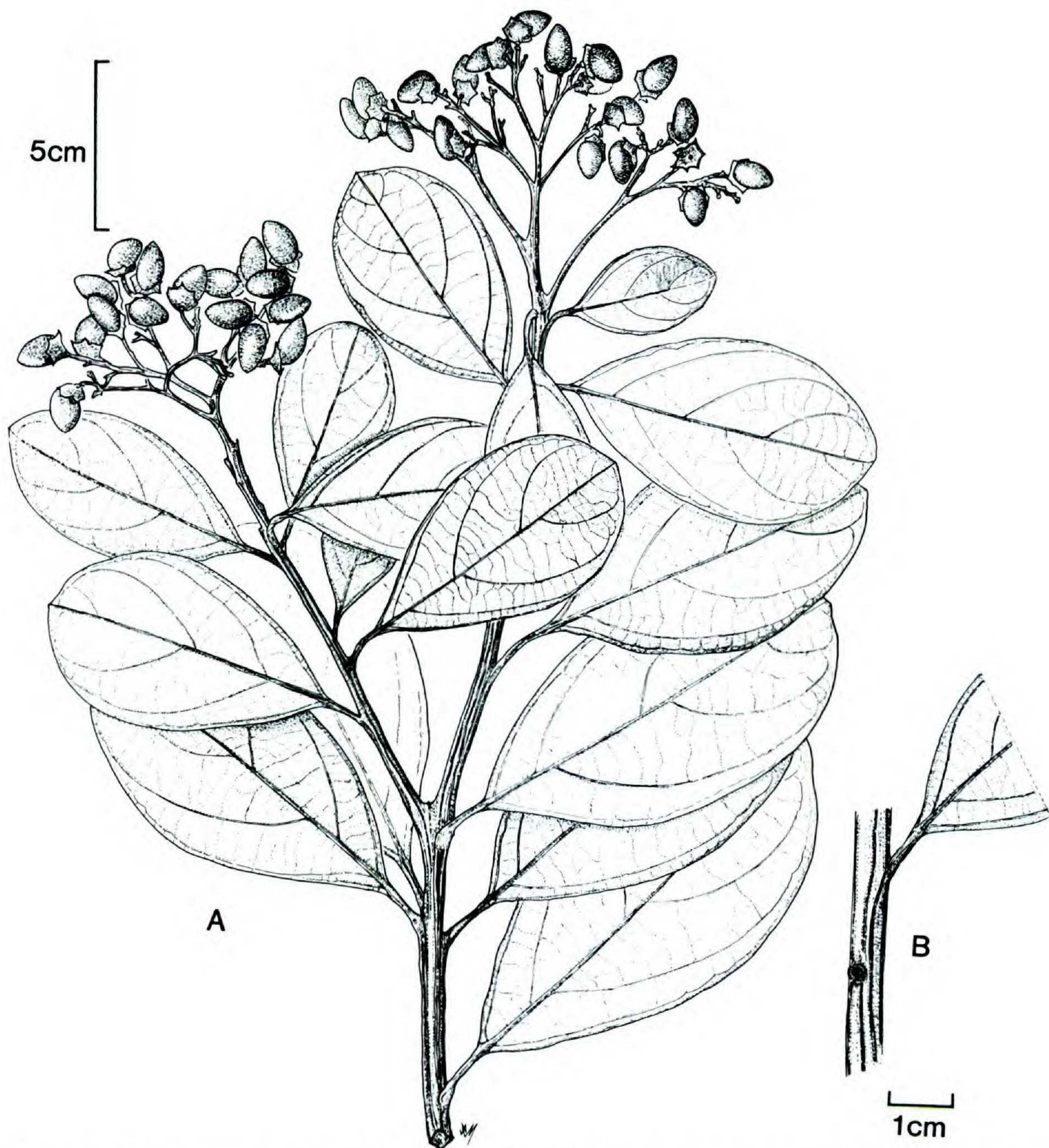


FIGURE 4. *Cordia leslieae*.—A. Fruiting branch.—B. Sub-alate twig with petiolar attachment. From Miller & Miller 886 (MO), Panamá, Panama.

long; ovary ellipsoid, 0.6–1 mm long; disc crateriform to nearly flat, thin, ca. 0.2 mm tall; style (2.1–) 2.5–3(–3.5) mm long, the stigma lobes filiform or nearly so. Fruits drupaceous, 3.5–4(–5) mm long, (2.6–)3–3.5(–5) mm broad, $\frac{2}{3}$ to nearly totally enclosed in the calyx, red, the stone ovoid to broadly ovoid, the endocarp bony.

Distribution. *Cordia linnaei* occurs in moist to wet forests from sea level to 900 m in elevation from Mexico to Colombia and in the West Indies. In Panama, *C. linnaei* is known from the Canal Area, Colón, Darién, Panamá, San Blas, and Veraguas.

This species was treated as *Cordia lineata* (L.) Roem. & Schultes in the *Flora of Panama* (Nowicke, 1969), as it has been in most recent works, but Stearn (1971) showed that this name is based on a long string of illegitimate names. It is easily recognized by its numerous, small, axillary inflorescences, which never branch cymosely as they do in *C. bifurcata*. The most likely Panamanian species with which *C. linnaei* could be confused is *C. inermis*, which has terminal and internodal, rather than axillary, inflorescences.

Additional specimens examined. PANAMA. CANAL AREA: near beach, at Ft. Kobbe, Duke 4195 (MEXU, MO); along abandoned road C29 just N of Las Cruces

Trail, 6 km E of Gamboa, 150 m, *Nee 9042* (MEXU, MO, US); Balboa, *Standley 25474, 26068, 29245* (US). COLÓN: 20 km from Transisthmian Highway on Santa Rita Ridge, SE facing slope, 400 m, *Knapp & Schmalzel 1765* (MO); Santa Rita Ridge, ca. 4–5.5 mi. E of Transisthmian Highway, *Lewis et al. 5267* (MO); lumber road at about 8 km NE of Santa Rita Ridge along ridge, 650 ft., *Wilbur & Weaver 10830* (DUKE); wooded slopes on Santa Rita Ridge about 5 mi. from highway at Sabanita, 650 ft., *Wilbur & Weaver 11827* (DUKE). DARIÉN: Chepigana, *Duke & Briston 264* (DUKE, MO); Isla Boca Grande, *Duke 8846* (MO). PANAMÁ: vicinity of Cerro Jefe, Altas de Pacora, 2,400 ft., *Antonio 3218* (MO); vicinity of Río Pacora, E of Panama City on Panama National Highway, *Bartlett & Lasser 16954* (MO); 3 mi. from Interamerican Highway on road to Cerro Campana, *Croat 12057* (F, MO, NY); Cerro Jefe, *D'Arcy 9748* (MO); Panamerican Highway at Río Mamonica, 4 mi. beyond Chepo, *Duke 5580* (GH, MO); grasslands on Cerro Campana, 2,400–2,700 ft., *Duke 8677* (DUKE, MO); end of road near Río Boquerón, road is 2 km N of cement plant on Colón Highway, ca. 26 km E of turnoff to end of road, 500 ft., *Hammel 915* (MO); summit of Cerro Jefe and forests along road beyond summit, *Hayden 1025* (MO); in woods near Panama, *Hayes 559* (K); Punta Paitilla, just E of Panama City, *Heriberto 212* (GH, US); Cerro Jefe, 4.8 mi. above Lago Cerro Azul, 600–800 m, *Miller & Miller 883* (MO); El Llano–Carti Road, 3 mi. from Panamerican Highway, 400 m, *Miller et al. 1016* (MO); El Llano–Carti Road, 5 km N of Panamerican Highway at El Llano, 300 m, *Nee 7902* (MO); Río Tapic, *Standley 28153* (US); Cerro Jefe, 850–900 m, *Sytsma 1959* (MO); slopes of Cerro Jefe beyond Cerro Azul between 4–8 mi. in mostly heavily wooded slopes, *Wilbur & Weaver 11348* (DUKE); between Pacora and Chepo, ca. 25 m, *Woodson et al. 1671* (MO). SAN BLAS: Permé, *Cooper 276* (F, GH, NY, US); hills SE of Puerto Obaldía, *Croat 16737* (MO (2), SCZ); through cultivation on mainland in front of Ustupo, *D'Arcy 9481* (MO); Malatuppi, Río Ibedi, *Duke 8487* (MO); along headwaters of Río Mulatupo, *Elias 1742* (MO); mainland opposite Playón Chico, 0–3 mi. from Caribbean, 0–200 m, *Gentry 6399* (MO); mainland opposite Playón Chico, 0–3 mi. from Caribbean, 0–200 m, *Gentry 6415* (MO); mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi. inland, *Lewis et al. 204* (MO, NY, UC, US). VERAGUAS: Isla de Coiba, *Dwyer 2323* (MO (2), US); 1–2 mi. above Santa Fe, *Gentry 3049* (F, MO, NY).

Cordia lucidula I. M. Johnston, J. Arnold Arbor. 21: 352. 1940. TYPE: Panama. Bocas del Toro: Potrero, Changuinola Valley, 20 Oct. 1923, *V. C. Dunlap 284* (holotype, US; isotypes, F, NY).

Tree to 5(–10) m tall, the twigs glabrous to sparsely strigillose. Leaves persistent; petioles (4–)7–12(–16) mm long, glabrous to strigillose; blades ovate to narrowly ovate, (9–) 11–22(–28) cm long, 5–9(–12) cm wide, the apex acuminate, the base obtuse and

slightly decurrent or rarely rounded or acute, the margin entire, the adaxial surface glabrous or rarely strigillose, the abaxial surface minutely strigillose rarely approaching glabrous. Inflorescence terminal or rarely internodal or axillary, cymose, 4.5–8.7 cm broad, the peduncle 1.8–3.7(–7.8) cm long, strigillose. Flowers sessile, monomorphic; calyx cuculate to campanulate, 3–4 mm long, ribs absent, glabrous to strigillose, the 3 lobes ± deltate, 0.8–1 mm long; corolla white, tubular with reflexed lobes, 5–7 mm long, 5-merous, the lobes oblong, 2.3–3 mm long, the tube 2.8–4.2 mm long; stamens 5, exserted, the filaments 4.5–7.5 mm long, the upper 2.4–3 mm free, pubescent at the point of insertion, the anthers ellipsoid to oblong, ca. 1.2 mm long; ovary ovoid, 1–1.3 mm long, glabrous; disc crateriform, ca. 0.7 mm tall; style 1.9–4.1 mm long, the stigma lobes clavate. Fruits 10–13 mm long, 9.5–12 mm broad, borne in the slightly expanded, cup-shaped calyx, drupaceous, red, the stone broadly inequilaterally ovoid, the surface ruminant and slightly ridged, the endocarp bony.

Distribution. *Cordia lucidula* occurs in wet forests from sea level to 1,500 m in elevation and ranges from Nicaragua to Panama. In Panama *C. lucidula* is known from the provinces of Bocas del Toro, Chiriquí, Darién, and Panamá.

Cordia lucidula is extremely variable and is the most commonly collected member of a difficult group of closely related species, including *C. lasiocalyx* and *C. porcata*, found in Panama and Costa Rica. *Cordia lucidula* can be distinguished by its three-lobed calyx, more or less ovate leaves, and bright red fruits without apical prolongation. Leaf shape and texture often vary on a single plant and with time of year and locality. *Cordia lucidula* differs from *C. lasiocalyx* by having an acuminate, rather than caudate leaf apex. *Cordia lucidula* is most likely to be confused with *C. porcata*, which differs in having white fruits and anthers more than 1.9 mm long.

Additional specimens examined. PANAMA. BOCAS DEL TORO: region of Almirante, *Cooper 372* (C, CFMR, F,

GH, US); Changuinola Valley, *Dunlap 356* (CFMR, F, US); Río Terebe just below Puerto Palenque, 350 ft., *Kirkbride & Duke 549* (F, MO, NY, SCZ); cloud forest of Cerro Bonyic, above Quebrada Hurón, 500–1,200 ft., *Kirkbride & Duke 596* (F, MO, NY, SCZ); Chiriquicito to 5 mi. S along Río Guarumo, *Lewis et al. 2089* (MO, UC); Chiriquí Lagoon, Fish Creek Hills, *Wedel 2394* (GH (2), MO), *2425* (GH, MO, US). CHIRIQUÍ: San Bartolo Limite near Costa Rican border, 12 mi. W of Puerto Armuelles, 400–500 m, *Croat 22150* (BR, C, CAS, F, LL, MEXU, MO, NY, RSA); Burica Peninsula, 8 mi. W of Puerto Armuelles, 200 m, *Liesner 353* (MO, WIS). COCLÉ: 7 km N of El Copé, *Folsom & Collins 6470* (NY). DARIÉN: primary forest along headwater of Río Tuqueza, ca. 2 km air distance from continental divide, in the vicinity of upper gold mining camp of Tyler Kittredge, *Croat 27126* (MO); trail from Pucuro to Cerro Mali, vicinity of mouth of Tapaliza River, ca. 100 m, *Gentry & Mori 13546* (MO, SCZ, US); 0–2 mi. E of Tres Bocas along the shortest headwater of the Río Cuasi, *Kirkbride & Duke 1184* (MO, NY). PANAMÁ: El Llano–Carti Road, 10.6 mi. from the Pan-American Highway, 400 m, *Miller et al. 871* (MO); El Llano–Carti Road, just south of San Blas border, 400 m, *Miller et al. 1014* (MO); El Llano–Carti Road, 10–12 km from junction with Inter-American Highway, 410 m, *Mori & Kallunki 2881* (AAU, MO, NY, U); El Llano–Carti Road, 8–11 km from Inter-American Highway, 300–400 m, *Mori 7709* (MO, U).

Cordia megalantha S. F. Blake, Proc. Biol. Soc. Wash. 36: 200. 1923; nom. nov. for *Cordia macrantha* S. F. Blake, Contr. U.S. Natl. Herb. 24: 19. 1922, non Chodat, 1921. TYPE: Guatemala. Izabal: Quebrada, 18 May 1919, S. F. Blake 7498 (holotype, US 989592).

Tree to 30(–60) m tall, the twigs glabrous. Leaves deciduous; petioles (8–)11–33(–55) mm long, glabrous; blades elliptic to obovate, (4.6–)6–19(–21) cm long, 2.9–8(–12.6) cm wide, the apex acute to acuminate or rarely obtuse, the base acute or rarely obtuse to rounded, the margin entire, the adaxial and abaxial surfaces glabrous. Inflorescence terminal, paniculate, to 30 cm broad, the branches glabrous except for puberulent tips. Flowers on short spurs 2–5 mm long, distylous; calyx tubular, (8.5–)9–10(–11) mm long, striate to 10–20 ribbed, glabrous to puberulent, the hairs dark brown, unevenly lobed, tearing upon dehiscence or dehiscing circumscissily; corolla marcescent, white, funnellform, 28–43(–50) mm long, the 5(–6) lobes deltate to ovate, 11–13 mm long; stamens 5(–6), the filaments 14.5–19 mm long,

the upper 5–10(–13) mm free, pubescent at insertion and frequently over the entire free portion, the anthers oblong, 2–4 mm long; ovary ovoid to conical, 1.3–2.5(–4) mm long; disc depressed ovoid, 0.5–1 mm tall; style 16–19 mm long, the stigma lobes clavate. Fruits enclosed by the persistent calyx and corolla, ellipsoid to narrowly ellipsoid, 8–12 mm long, 4–6 mm broad, the wall thin, fibrous.

Distribution. *Cordia megalantha* ranges along the Atlantic coast of Central America in wet forests from sea level to 400 m in elevation. Disjunct populations occur on the Pacific side of Central America on the Osa Peninsula of Costa Rica and the Burica Peninsula in Chiriquí where the only known collection from Panama was made.

Often exceeding 30 m in height, *Cordia megalantha* is the tallest Central American species of *Cordia*. Although there are no reports of *C. megalantha* being cultivated as a timber tree, as is *C. alliodora*, it may have potential in wet regions. It apparently does not flower each year (T. Wendt, pers. comm.) and this, combined with its height, may be responsible for the paucity of collections. *Cordia megalantha* is very distinctive among the Panamanian members of the genus in its large size, marcescent corolla, and deltate corolla lobes.

Additional specimens examined. PANAMA. CHIRIQUÍ: west of San Bartolo Limite near Costa Rican border, *Croat 22175* (MO).

Cordia panamensis Riley, Kew Bull. 1927: 135. 1927. TYPE: Panama. Panamá: secondary growth at sea level near Old Panama, L. A. M. Riley 143 (holotype, K; isotypes, MO, US).

Tree to 10(–15) m tall, the young twigs hirsute. Leaves persistent; petioles (5–)7–12(–17) mm long, villous to hirsute or occasionally strigillose and with scattered, erect, longer hairs; blades dimorphic, the larger ones ovate to ovate-elliptic, (12–)17–28(–35) cm long, (5–)6.5–13.5(–15) cm wide, the apex

acuminate, the base obtuse to rounded or occasionally somewhat cordate, often somewhat asymmetrical, the smaller ones orbicular, (5-) 6.5-9(-10) cm long, (3.8-)5-8.4(-10) cm wide, the margin entire, the adaxial surface scabrous, the abaxial surface \pm pubescent, the hairs stiff but not rough to the touch, nearly erect to spreading. Inflorescence terminal or in the axils of the branches, cymose, (5-)7-13.5(-16) cm broad, the lower portion of the branches villous to hirsute, the tips of the branches densely strigillose. Flowers sessile, unisexual by abortion, the plants dioecious, the male flowers with reduced styles, the female flowers with small, nonfunctional anthers. Female flowers with a tubular calyx 2-3.6 mm long, ribs absent, strigillose, the 3-5 lobes unevenly deltate to triangular, 0.4-0.6(-1) mm long; corolla white, tubular with reflexed lobes, 3.8-4.5(-5.5) mm long, (4-) 5(-6)-merous, the lobes oblong-ovoid, 1-1.8 mm long, the tube (2-)2.5-3(-3.7) mm long; stamens (4-)5(-6), the filaments 3-3.6(-4.3) mm long, the upper 0.4-1.1 mm free, glabrous, the anthers ellipsoid, shriveled and containing only aborted pollen, ca. 0.3 mm long; ovary ellipsoid, 1-1.3(-1.8) mm long, glabrous; disc scarcely distinct from the base of the ovary; style 2-3.4(-4) mm long, the stigma lobes discoid. Male flowers with a campanulate calyx (2.5-)3-4 mm long, ribs absent, strigillose, the 3-5 lobes uneven, deltate to triangular, 0.7-1.1 mm long; corolla white, tubular-campanulate with reflexed lobes, 4.5-6(-6.5) mm long, 5(-6)-merous, the lobes oblong-ovoid, (1.5-)2-2.3(-2.7) mm long, the tube (1.5-)2.5-3.9 mm long; stamens 5(-6), the filaments 4.8-7.2 mm long, the upper 2-3.5(-4.3) mm free, villous at the point of insertion, the anthers ellipsoid, 0.8-1.3 mm long; ovary ovoid, 0.6-1.2 mm long, glabrous; disc crateriform, 0.5-0.7 mm long; style abortive, 1-2(-3.3) mm long, the stigma lobes filiform. Fruits seated in the cupulate calyx, white, drupaceous, glabrous, the stone inequilaterally ovoid, 6-7.5 mm long, (4.3-) 5.5-6 mm broad, the endocarp bony.

Distribution. *Cordia panamensis* occurs in dry to wet forests and ranges from southern Mexico to northern South America from sea level to 1,000 m in elevation. In Panama it is known from all regions except Bocas del Toro.

The *Cordia panamensis* complex is one of the most taxonomically difficult groups in the genus. Its Central American members, which include *C. anisophylla* and *C. cymosa*, are similar in appearance and are sometimes sympatric. The group reaches its greatest diversity in Panama and northern South America. *Cordia panamensis* differs from *C. cymosa* by being smaller in all aspects and by having only simple (vs. echinate) hairs. It differs from *C. anisophylla* in having a shorter corolla and fruits that are nearly as broad as long. *Cordia panamensis* is extremely variable in Panama with individual populations differing considerably in leaf size, shape, and indument. North of Costa Rica, it is more constant morphologically. *Cordia panamensis* is most closely related to *Cordia hebeclada* I. M. Johnston of Colombia, Ecuador, and Peru, which differs only in its evenly velutinous twigs and lower leaf surfaces.

Additional specimens examined. PANAMA. CANAL AREA: Juan Mina, *Bartlett & Lasser 16523* (DUKE, MO); beside railroad tracks along road to Tropic Test Center Miraflores Annex, *Correa 261* (DUKE, MO); Guillard Highway near Paraiso, *Croat 10141* (MO, SCZ); Barro Colorado Island, *Croat 10250* (MO, UC), *10390* (DUKE, F, MO, NY, SCZ, UC); Ancon Hill near gates to Quarry Heights Military Preserve rear gate, *Croat 11950* (F, MO, SCZ); Barro Colorado Island, *Croat 11967* (DUKE, F, MO, NY, SCZ); road S-11, NW of Escobal, *Croat 12460* (MEXU, MO (2)); Road K-2G, *Croat 15142* (MO); roadside in forest between Gatún and Fort Sherman, *Croat 15400* (MO); Pipeline Road 2 mi. from Gamboa gate, *Croat 16612* (MO); vicinity of Madden Lake along Boy Scout Road, less than 100 m, *Croat 38322* (MO); near Pedro Miguel railway station, *D'Arcy & D'Arcy 6021* (CHAPA, MO (2), RSA, US (2)); near beach at Ft. Kobbe, towards Vera Cruz, *Duke & Mussell 6559* (F, MO); Farfan Beach, *Dwyer 6766* (MO); Barro Colorado Island, *Foster 972* (DUKE, F), *1916* (DUKE, F, MO); Curundu Air Force Survival School, *Gentry 1464* (MO); Cerro de Ancon, *Gervais 133* (F, US); without definite locality, *Johansen 3* (US); Fort San Lorenzo, area W of Limón Bay, Gatún Locks and Gatún Lake, *Johnston 1515* (A (2)); Barro Colorado Island, *Kenoyer 632* (MO); Ancon Hill, 100-200 m, *Killip 12113* (US); 1 mi. W of the

junction of the Cocosolo Hospital and the lookout to Gatún Lake, *Lazor & Blum 5377* (MO); Fort Kobbe Military Reservation, *Luteyn 1087* (DUKE, F, MICH, MO); Balboa, *Maxon 6926* (US); Pipeline Road, 10–15 mi. from Gamboa, 100 m, *Miller 1028b* (MO); Summit Gardens, 0–100 m, *Mori & Kallunki 1777* (MO); along road to golf course along Chagres River, Gamboa, 30 m, *Nee 7378* (ENCB, L, MEXU, MO, NY, RSA, US); along road to Radar Station on Semaphor Hill, 1 km N of Summit Garden, 100–150 m, *Nee 7493* (DUKE, MO, POM, US); Gamboa, *Pittier 3708* (NY, US); vicinity of Río Cocoli, Road K9, *Stern et al. 328* (G, MO, UC, US); observatory at Miraflores Locks, 75 m, *Sullivan 608* (MO); Albrook Air Force Base, *Tyson 1114* (MO, SCZ); Fort Clayton, Farfan Beach area, *Tyson 1823* (MO, SCZ); Curundu near Survival School, *Tyson 4174* (MO, SCZ); Miraflores on road to water plant, *Tyson 6596* (DUKE, MO); along Pipeline Road, 3 mi. NW of Gamboa, 100–200 ft., *Webster 16768* (MO); Balboa, *Wheeler s.n.* (GH); vicinity of Miraflores, *White 134* (F, MO); near lake opposite the island, *White 125* (F, MO). CHIRIQUÍ: pastures and forested river banks east of Gualaca, 500 ft., *Allen 5032* (MO); Progreso, *Cooper & Slater 317* (CFMR, F, US); Burica Peninsula, Dist. Guanabano, disturbed areas along Quebrada Quanabaro, *Croat 22530A* (MO); 2 mi. SW of Guabala, *Tyson et al. 4247* (MO); vicinity of Puerto Armuelles, *Woodson & Schery 814* (MO, US). COCLÉ: Río Hato Airstrip, *Blum & Dwyer 2471* (MO, SCZ); between Las Margaritas and El Valle, *Woodson et al. 1296* (F, MO, NY). COLÓN: entre Colón y Portobelo, 5 m, *Holderidge 6440B* (DUKE, MO); Tres Brazos sawmill, Icacal, which is in between Salud y Boca de Río Indio, *Howell 48* (MO); Salud, *Lao & Holderidge 222* (MO); Nuevo Chagres, beach and adjacent roadside, *Lewis et al. 1858* (ENCB, MO); along the beach between Fato and Playa de Damas, *Pittier 3932* (US), 3982 (NY). DARIÉN: about 10 mi. S of El Real on Río Pirre (House no. 22), *Duke 5482* (MO, NY); Río Pirre, *Duke 8248* (MO); Río Pucro, below village of Pucro, *Duke 13125* (F, MO, NY); 4.5 km S of El Real, along dry stream bed of Río Uruseco, *Mori & Kallunki 5372* (AAU, MO, NY); 3 mi. E of Santa Fe, *Tyson et al. 4676* (DUKE, MO, SCZ). HERRERA: entre Tres Puntas y Chepo (Las Minas), *Carrasquilla & Lao 340* (MO); Llano de las Minas, 350 m, *Lao 47* (MO). LOS SANTOS: Las Tablas, *Dwyer 1159* (MO). PANAMÁ: hills south of El Valle de Antón, 700 m, *Allen 2481* (MO, US); Trapiche, Perlas Islands, *Allen 2613* (MO); San José Island, *Anderson s.n.* (NY); out C-15 road, just outside the zone, *Blum & Dwyer 2677* (MO, SCZ); roadside on way to Cerro Campana, ¼ mi. from highway, *Croat 12030* (MEXU, MO, NY); Cerro Campana, along road above FSU cabin, *Croat 14207* (MO (2), SCZ); between Cerro Azul and Cerro Jefe, *Dressler 3865* (DUKE, F, MO); El Llano–Carti Road, 12–14 km N of El Llano, *Dressler 4359* (DUKE, ENCB, F, MO); vicinity of El Llano, *Duke 5813* (MO); Río San Tomas, *Duke & Mussell 6650* (AAU, MO); grassland on Cerro Campana, 2,400–2,700 ft., *Duke 8667* (MO, US); Isla de Pedro Gonzales, *Dwyer 1705* (MO); Tocumen, thicket near airport, *Dwyer 4044* (US); San José Island, *Erlanson 226* (MICH, US), 276 (G (2), NY, US), 446 (US); Cerro Campana, near tower, *Folsom et al. 2312* (MO); adjacent to Ft. Clayton, 50 m, *Haines 564* (DUKE

(2), MO); San José Island, near Punta del Cabo, *Harlow 17* (GH, US); in woods about Panama, *Hayes 89* (BR); San José Island, *Johnston 51* (GH (2), MO, US), 79 (GH); Bella Vista, sea level, *Killip 12014* (GH, NY, US); low woods E of Bella Vista, a suburb of Panama City, *Maxon & Valentino 6962* (US); S of Farfan beach along shore and adjoining road, sea level, *Miller & Hamilton 730* (MO); along the road to Cerro Campana, 600 m, *Miller et al. 738* (MO); along the road to Cerro Campana, 1–3 mi. from the Pan-American Highway, *Miller & Miller 959, 961* (MO); along the road to Cerro Campana, ca. 5 mi. from the Pan-American Highway, *Miller & Miller 1000* (MO); Morro Island, just off N shore of Taboga Island, *Mori et al. 4074* (AAU, MO, NY, WIS); Bella Vista, *Standley 25347* (MO, US); near the big swamp E of Río Tocumen, *Standley 26647* (US); near Matias Hernández, *Standley 28877* (US); Punta Paitilla, *Standley 30816* (US); between Matias Hernández and Juan Diaz, *Standley 32039* (US); Archipelago de Las Perlas, San José Island, coast beside La Bodega, *Stimson 5323* (DUKE, SCZ (2)); Taboga Island near village, Perlas Islands, *Tyson 5593* (DUKE, SCZ); wet savanna E of Pacora, 25 m, *Woodson et al. 757* (F, MO, NY); Isla Taboga, *Woodson 1544* (MO, NY), *Woodson et al. 1547* (F, NY). SAN BLAS: Mulatuppu, *Duke 8540* (MO); Ailigandi, *Dwyer 6827* (MO). VERAGUAS: Isla de Coiba, *Dwyer 1574* (F, MO), 2343 (BR, MO (2), SCZ); Cerro Tute, 1,000 ft., *Dwyer 4293* (US), 4335 (MO); Santiago, 4 mi. from Transisthmian Highway toward Atalaya, *Dwyer & Kirkbride 7412* (MO (2), NY, UC); southern shore of Ensenada Santa Cruz, northern tip of Coiba Island, *Foster 1626* (DUKE (2), F).

Cordia porcata Nowicke, *Phytologia* 18: 397. 1969. TYPE: Panama. Colón: Santa Rita Ridge lumber road, 3 Oct. 1968, *M. Correa A. & R. Dressler 1076* (holotype, MO 2062961; isotype, MO).

Shrub or small tree 2–6 m tall, the twigs glabrous. Leaves persistent; petioles 5–11 mm long, broadly canaliculate adaxially, glabrous; blades narrowly elliptic to lance-elliptic, (5–)8.3–21(–24) cm long, 3–7.5(–10) cm wide, the apex acuminate, the base acute or rarely obtuse, slightly decurrent, the margin entire, sometimes slightly revolute, the adaxial surface glabrous, often drying with a silvery sheen, the abaxial surface glabrous to sparsely and minutely strigillose. Inflorescence terminal or internodal, cymose, 2.5–5.5(–10) cm broad, usually with 50–100 flowers, the peduncle 1.8–4.4 cm long, the branches canescent to strigillose, the hairs brown. Flowers monomorphic, sessile; calyx campanulate, 5.2–6.5 mm long, 2.6–5 mm

wide at the mouth, ribs absent, nearly glabrous to minutely strigillose, the (2-)3(-4) lobes \pm deltate, 1.3-1.8 mm long; corolla white, tubular with reflexed lobes, 6.5-10 mm long, (4-)5-merous, the lobes oblong, 3.1-4.5 mm long, 1.5-2 mm wide, the tube 3.7-6.4 mm long; stamens (4-)5, the filaments (4.5-)7-8.4 mm long, the upper (1.3-)2.5-4 mm free, the lower free portion pubescent, the anthers narrowly oblong, 1.9-2.3 mm long; ovary ovoid to broadly ovoid, 0.8-1 mm broad, glabrous; style (4-)5.2-5.8 mm long, the stylar branches 2-2.5 mm long, the stigma lobes clavate. Fruits borne in the slightly expanded, saucer-shaped calyx, white at maturity, drupaceous, glabrous, the stone inequilaterally ovoid and sharply apiculate at the apex, 8.7-11 mm long, 4.8-6.5 mm broad, essentially smooth, the endocarp bony.

Distribution. *Cordia porcata* occurs in wet forests and ranges from southern Nicaragua to Panama from sea level to 1,500 m in elevation. In Panama it is known from the provinces of Coclé, Colón, Los Santos, and Panamá.

Cordia porcata differs from *C. lucidula*, the species with which it is most likely to be confused, in having lance-elliptic leaves, anthers more than 1.9 mm long, and smooth, rostrate fruits. Although *C. porcata* is quite common in some areas of Panama, it is known from only a small number of collections in northern Costa Rica and a single collection from Nicaragua.

Additional specimens examined. PANAMA. COCLÉ: region N of El Valle de Antón, 1,000 m, *Allen 3710* (BR, F, G, MO, U); Cerro Pilón, above El Valle de Antón, *Croat 14323* (MO, NY); La Mesa above El Valle, along road which ends in pasture, 810 m, *Croat 25310* (MO, NY); Cerro Pilón, El Valle, 3,000 ft., *Duke & Lallathin 15015* (MO); vicinity of La Mesa, N of El Valle, 1,000 m, *Gentry 6813* (AAU, MO, NY). COLÓN: Cerro Santa Rita, ca. 6 mi. from the Transisthmian Highway, 800-900 ft., *Antonio 1805* (MO); Santa Rita Ridge Road, ca. 1 hour walk from end of road, *Antonio 4490* (MO); East Santa Rita Ridge, *Correa & Dressler 635* (MO, SCZ); Santa Rita Ridge, *Correa & Dressler 1076* (MO), *Croat 13837* (MO), *D'Arcy & D'Arcy 6169* (C, F, MO); Santa Rita lumber road, ca. 15 km E of Colón, *Dressler & Lewis 3702* (F, MO, US); Santa Rita Ridge, *Dwyer 8581* (F, MO); Santa Rita Ridge, highway to 8 mi. east, 800

ft., *Dwyer et al. 9027* (MO (2), NY); Santa Rita Ridge, *Dwyer & Gentry 9366* (MO, NY), *9373* (MO); near Agua Clara rainfall station, Santa Rita Ridge, *Foster 1730* (DUKE); Santa Rita Ridge, 2-3 mi. from Transisthmian Highway, *Gentry 1865* (MO); Santa Rita Ridge, E ridge, *Gentry & Dwyer 4816* (DUKE, F, MO, RSA); Santa Rita Ridge east of Transisthmian Highway, 300-500 m, *Gentry 6546* (F, MO); Santa Rita Ridge, 400-500 m, *Knapp et al. 1680* (MO); end of Santa Rita Ridge Road, 21 km from Transisthmian Highway, 400-500 m, *Knapp & Schmalzel 5243* (MO); Santa Rita Ridge Road, 21-26 km from Transisthmian Highway, 500-550 m, *Knapp 5867* (MO); Santa Rita Ridge, 2 mi. from Transisthmian Highway, 100 m, *Lao et al. 7* (F, MO (2)); Santa Rita Ridge, ca. 5.5-6 mi. E of Transisthmian Highway, *Lewis et al. 5391* (MO, UC); *Lewis 5397* (F, MO, NY); Santa Rita Ridge trail, beyond end of Santa Rita Ridge Road (Panamanian Highway R 20 D), 17-35 km from Boyd-Roosevelt Highway, 400-800 m, *Mori & Crosby 6308* (MO, US); Santa Rita Ridge Road, 7.8 km from the Boyd-Roosevelt Highway, ca. 25 km W of Colón, *Mori & Dressler 7906* (AAU, MO, NY); 2.7 mi. by gravel road, NE of carretera Transisthmica, on the Santa Rita Ridge, *Nee & Mori 3676* (MO, WIS (2)); Santa Rita Ridge, end of road from Transisthmian Highway, ca. 10 mi. from highway, *Porter et al. 4762* (MO); Santa Rita, *Suere & Dressler 4818* (MO); Santa Rita Ridge road, 20 km from Transisthmian Highway, 100-1,200 ft., *Sytsma 1094* (MO); Santa Rita Ridge, 20 km from Transisthmian Highway, *Sytsma 1108* (MO); Santa Rita Ridge Road, 20-22 km from Transisthmian Highway, 1,000-1,200 ft., *Sytsma 1311, 1312* (MO); Santa Rita Ridge, *Sytsma 1548* (MO); upper Río Piedras headwaters, along trail from end of Santa Rita Ridge Road, ca. 11 km SW of Cerro Bruja, 600-700 m, *Sytsma et al. 4184* (MO). LOS SANTOS: Cerro Pilón, 2,700 ft., *Dwyer & Lallathin 8586* (MO). PANAMÁ: El Llano-Carti Road, 13.7 km N of Pan-American Highway, *Folsom 3589* (MO).

Cordia protracta I. M. Johnston, J. Arnold
Arbor. 21: 349. 1948. TYPE: Panama.
San Blas: Permé, *G. P. Cooper 244* (holotype, GH; isotypes, F, MICH, NY, US (2)).

Tall shrub, the twigs sparsely strigillose. Leaves persistent; petioles 4-9 mm long, canaliculate adaxially, sparsely strigillose; blades anisophyllous, falcate, the larger oblong-ovate, 15.6-24.6 cm long, 5.4-10.3 cm wide, the apex long acuminate, the acumen to 3 cm long, the base asymmetrical, rounded to obtuse, the margin entire to slightly undulate, the adaxial surface glabrous, the abaxial surface glabrous but sparsely strigillose along the veins. Inflorescences terminal or borne in the branch axils, few per stem, cymose, to 6.5 cm long, 4.5 cm broad, with 20 or more flowers, the branches strigillose. Flowers ses-

sile or nearly so, bisexual, monomorphic; calyx tubular, 7–7.5 mm long, ca. 4 mm wide at mouth, ribs absent, sparsely strigillose, the 5 lobes deltate, ca. 1 mm long; corolla white, tubular with reflexed or spreading lobes, ca. 12 mm long, 5-merous, the lobes oblong to ovate, 4–4.5 mm long, ca. 2.5 mm wide, the tube 7–7.5 mm long; stamens 5, exserted, the filaments ca. 11 mm long, the upper 4–4.5 mm free, slightly puberulent at insertion, the anthers oblong, ca. 2.2 mm long; ovary narrowly ovoid, ca. 2.0 mm long, ca. 1.1 mm broad, glabrous; style ca. 7.5 mm long, the stylar branches ca. 2.5 mm long, the stigma lobes clavate. Fruits borne in the slightly accrescent saucer-shaped calyx, white, drupaceous, glabrous, the stone inequilaterally ovoid, 10–11 mm long, 6–7 mm broad, ruminant, the endocarp bony, 1-locular.

Distribution. *Cordia protracta* is known only from wet forests at low elevations along the coast of San Blas and Chocó provinces in Colombia.

Cordia protracta is known from only a few localities in Panama. A distinctive species, it is perhaps most closely related to *C. correae* but differs by having falcate, shiny leaves, and white fruits. Further, *C. correae* occurs at high elevations in cloud forests in contrast with the lowland wet forests inhabited by *C. protracta*.

Additional specimens examined. PANAMA. SAN BLAS: vicinity of Puerto Obaldía, *Croat 16873* (MO (2)); Mulatuppu, Río Ibedi, *Duke 8483* (MO); 3–4 hours up Río Mulatupo by foot, *Kirkbride 233, 234* (MO).

***Cordia sebestena* L., Sp. Pl. 190. 1753.**

TYPE: without locality or collector's name (holotype, LINN (Savage Catalog number 253.2), not seen; microfiche, MO).

Cordia speciosa Salisb., Prodr. Stirp. Chap. Allerton 111. 1796. TYPE: not seen.

Small tree or shrub to 8 m tall, the twigs glabrescent. Leaves persistent; petioles (1.0–) 1.5–3.8(–4.5) cm long, pubescent, the hairs simple, appressed; blades ovate, (7–)9–20(–22) cm long, (4.5–)6–12(–14) cm wide,

the apex acute, the base rounded to obtuse, rarely somewhat cordate, often slightly uneven, the margin entire or occasionally slightly undulate, the adaxial surface scabrous, the hairs from a basal cystolith, the abaxial surface nearly glabrous with hairs sparse and restricted to the veins. Inflorescence subterminal, cymose, 6.5–12 cm broad, with 12–45 flowers, the branches strigillose. Flowers on pedicels 4–6 mm long, distylous; calyx tubular-campanulate, 11–24 mm long, ribs absent, glabrous or with an indument of 2 types of hairs, the first type simple and straight, 0.4–0.6 mm long, appressed, white to translucent, the second type simple, curly, 0.2 mm long or shorter, brown, usually 2-lobed but sometimes with up to 5 irregular and uneven lobes; corolla bright reddish orange, funnelform, 30–58 mm long, 5–7-merous, the lobes ovate to very widely ovate, 8–10 mm long; stamens 5–7, the filaments 22–33 mm long, the upper 2–6 mm free, glabrous, the anthers oblong, 2.8–3.8 mm long; ovary conical, 1.5–3 mm long; style 13–35 mm long, the stigma lobes clavate. Fruits completely enclosed in the accrescent calyx and often extending in a thin tip up to 12 mm beyond the fruit, drupaceous, white, the stone ovoid, 2–4 mm long, 1.5–2.3 cm wide, the endocarp bony.

Distribution. *Cordia sebestena* is basically pan-Caribbean in distribution, occurring from southern Florida through the West Indies, and to the Atlantic coast of southern Mexico, Central America, and northern South America. It grows along coastal strands and is particularly common on the offshore islands of Central America. In Panama it appears to be native only in the Comarca de San Blas.

Cordia sebestena is grown ornamentally throughout warm areas of the world for its bright orange-red flowers. It is the only Panamanian species of sect. *Cordia* and is distinctive in its large, funnelform corolla and large, drupaceous fruits completely enclosed by the accrescent calyx. The fruits are edible and are very sweet, although quite mucilaginous.

Additional specimens examined. PANAMA. PANAMÁ: San Francisco de la Caleta (atras del S.A.S.), *Carrasquilla* 178 (F, MO) (probably cultivated). SAN BLAS: Isla Soskatupu, *Duke* 8963 (MO, US), 15476 (MO); Guadia Tupo, *Dwyer* 6864 (MO (3)); 50 mi. W of Ailigandi, on SW shore, *Edwards* 1 (F, MO); Soskatupu Island, 0–150 m, *Elias* 1698 (MO); small coral island NW of Ailigandi, *Hammel & D'Arcy* 5051 (MO); Playón Chico and vicinity, Pinkanti hillside near bay, *Stier* 186 (MO); Playón Chico and vicinity, Yantuppu, *Stier* 192 (MO).

***Cordia spinescens* L.**, Mant. Pl. 2: 206. 1771; I. M. Johnston, J. Arnold Arbor. 30: 103. 1949. TYPE: based on a collection from “*India orientali*” (cf. Johnston, 1949a) (holotype, LINN (Savage Catalog number 253.2), not seen; microfiche, MO).

Varronia ferruginea Lam., Tab. Encyc. 1: 418. 1791; Poir., Encyc. 4: 263. 1797; Desv., J. Bot. (Desvaux) 1: 266, t. 9. 1809; *Cordia ferruginea* (Lam.) Roemer & Schultes, Syst. Veg. 4: 458. 1819. TYPE: based on plants cultivated in Paris (holotype, P-JU, number 6525a, not seen; microfiche, MO).

Cordia riparia Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 71, t. 207. 1818; I. M. Johnston, J. Arnold Arbor. 30: 103. 1949. TYPE: Colombia: Mompox, Magdalena Valley, no collector named on specimen (holotype, P in herb. Humboldt, not seen; microfiche, MO).

Cordia laxiflora Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 72. 1818; I. M. Johnston, J. Arnold Arbor. 30: 103. 1949. TYPE: Colombia: between Mompox and Morales, Magdalena Valley, no collector named on specimen (holotype, P in herb. Humboldt, not seen; microfiche, MO).

Cordia schomburgkii DC., Prodr. 9: 490. 1845. TYPE: Guyana. Without definite locality: 1838, *Schomburgk* 406 (holotype, G-DC, not seen; microfiche, MO).

Cordia thibaudiana DC., Prodr. 9: 489. 1845. TYPE: without locality or collector (holotype, G-DC, not seen; microfiche, MO).

Cordia pauciflora Rusby, Mem. Torrey Bot. Club 6: 83. 1896. TYPE: Bolivia: near Cochabamba, *Bang* 1291 (not seen).

Cordia costaricensis I. M. Johnston, J. Arnold Arbor. 30: 103. 1949. TYPE: Costa Rica. San José: vicinity of El General, 1,190 m, Aug. 1936, *A. F. Skutch* 2828 (holotype, GH; isotypes, K, MICH, MO, NY, US).

Shrub 1–3(–6) m tall, the branches arching to sprawling, the twigs puberulent to hirsute. Leaves deciduous, on slightly recurved spurs 1.5–3(–4) mm long; petioles (1–)3–11(–15) mm long, puberulent to hirsute; blade ovate to elliptic-ovate, (3–)4–11.5(–14) cm long, (1.4–)2–6.5(–7.8) cm wide, the apex

acute to attenuate or slightly acuminate, the base obtuse to rounded, the margin coarsely serrate to minutely denticulate, the adaxial surface scabrous to scabrid, rarely merely papillose, the abaxial surface puberulent to tomentulose, sometimes with most of the hairs restricted to the veins. Inflorescences axillary, spicate, (1.3–)2.5–8.5(–11.5) cm long, 4–7(–9) mm broad, the peduncle adnate to the petiole at the base, (1–)2–4.5(–6.5) cm long, puberulent to hirsute. Flowers sessile, distylous; calyx campanulate, (1.8–)2.3–3.5(–4.2) mm long, ribs absent, strigillose to puberulent and usually with small, globose wax particles, the 5 lobes deltate to shallowly triangular; corolla white, tubular, (3–)3.8–5.4(–6.2) mm long, truncate to frilled at the apex, the tube (1.7–)2–2.7(–3.1) mm long; stamens 5(–6), the filaments (2.7–)3.3–5(–6.2) mm long, the upper (0.5–)1–2(–2.4) mm free, puberulent just beneath the point of insertion, the free portion glabrous, the anthers ellipsoid, 0.6–0.8(–1) mm long; ovary ovoid to broadly ovoid, 0.7–1.3 mm long; disc crateriform to annular (0.2–)0.4–0.6(–1.1) mm tall or enclosing the entire surface of the ovary; style (1.5–)2–4(–4.8) mm long, the stigma lobes clavate. Fruits drupaceous, ½ to nearly completely enclosed in the slightly accrescent calyx, red, 3.7–4.1 mm long, (2–)2.7–3.3 mm broad, the stone ovoid to broadly ovoid, the endocarp bony.

Distribution. *Cordia spinescens* is a very widespread, weedy species that occurs from Central Mexico into South America, although it is apparently absent in the West Indies. It grows from sea level to 2,000 m in elevation in a wide variety of habitats. In Panama it is known from all regions except Los Santos.

Cordia spinescens is extremely variable but is easily recognized by its axillary spicate inflorescences with the base of the peduncle adnate to the petiole of the subtending leaf. This is the most commonly collected species of *Cordia* in Mexico and Central America. *Cordia spinescens* is often found in open disturbed areas and is very common in moist ditches along roadsides. Unlike the other

shrubby species of sect. *Varronia* that usually have a rather erect form of growth, *C. spinescens* often has long arching branches.

The species of sect. *Varronia* characterized by spicate inflorescences, three of which occur in Central America, make up the most complex group in the entire genus (discussion under *C. curassavica*). This assemblage is centered in the Andes, and numerous species have been described from this region, although some should certainly be placed in synonymy. As a group, they are phenotypically plastic, and apparently all of the species involved are interfertile. Since most species of sect. *Varronia* with spicate inflorescences are widespread, natural hybridization is common, which has contributed to the confusion surrounding this group. As defined here, *Cordia spinescens* has its closest relatives in South America in *Cordia multispicata* Cham., and perhaps in the West Indies in *Cordia brownei* (Friesen) I. M. Johnston.

There is extreme morphological variability between populations of *Cordia spinescens*. Plants from low to middle elevations have ovate leaves with acute to slightly acuminate apices and elongate spikes in the axils of fully expanded leaves with the peduncle adnate to the petiole. At higher elevations in Panama and Costa Rica, the plants have more attenuate leaves, and the spikes appear well before the leaves are expanded, often giving the appearance of a panicle rather than spicate inflorescence. These are not true panicles, however, since as flowering proceeds, the leaves expand and the inflorescence structure thus becomes the same as in plants from lower elevations. This variant from the uplands of Panama and Costa Rica was originally described by Johnston (1949a) as *Cordia costaricensis*, and the type (*Skutch 2828*) as well as several collections made at a similar stage of development differ from the more typical lowland plants in having shorter, broader spikes with more crowded flowers, more acuminate calyx lobes, more attenuate leaf apices, more prominently serrate leaf margins, and evenly hirsute or velutinous stems. However, intergradation between these

upland populations and typical *C. spinescens* is so extensive that more intermediates are observed throughout their combined range than are individuals exhibiting characters of the extremes. These intermediates do not exhibit any reduction in pollen stainability and there is no evidence of habitat differentiation between them and either of the extremes.

With a species as variable as *Cordia spinescens*, it is not surprising that there has been considerable nomenclatural confusion. The name *Cordia ferruginea* (Lam.) Roemer & Schultes was widely applied by earlier authors, although Johnston (1949a) correctly pointed out that the Linnaean name *C. spinescens* has priority and must be accepted. The types of these two names are clearly conspecific, despite the fact that Linnaeus mistakenly described *C. spinescens* as East Indian; no species of sect. *Varronia* are native in the Old World. This confusion probably resulted from the fact that *C. spinescens* had been cultivated in Europe at least as early as the late eighteenth century, as indicated by Johnston (1949a), suggesting that Linnaeus probably based his description on a cultivated specimen. Lamarck clearly based his description of *Varronia ferruginea* on plants that were cultivated in Paris in 1791.

Additional specimens examined. PANAMA. BOCAS DEL TORO: along railroad track near station at Milla 5, *Croat 16485* (F, MO); Changuinola Valley, *Dunlap 280* (US), *281* (GH); Changuinola Valley, Isla Potrero, *Dunlap 460* (CFMR, F); upper Río Changuinola, few miles upstream from Changuinola, *Dwyer 4385A* (MO); trail leading to ridge above Almirante, *Gentry 2758* (F, MO, NY); Río San Pedro, *Gordon 48* (MO); Chiriquí border along continental divide on carretera del Oleoducto ca. 1 km N of Quebrada Arena, IRHE Fortuna Hydro Electric Project, 1,150 m, *Knapp 5085* (MO); Changuinola to 5 mi. S at junction of ríos Changuinola and Terebe, 100–200 ft., *Lewis et al. 845* (K, MO, UC, US); Almirante, near road to Chiriquí, ca. 200 ft., *McDaniel 5075* (MO); Chiriquí Lagoon, Water Valley, *Wedel 1633* (MO, US), *1672* (MO), *1801* (GH, MO); Chiriquí Lagoon, Old Bank Island, *Wedel 2169* (MO, US); Quebra Nigua, *Wedel 2741* (MO, US); Chiriquí Lagoon, Isla Colón, *Wedel 2839* (MICH, MO, NY, US). CANAL AREA: Barro Colorado Island, *Aviles 103* (MO); *Bangham 495* (F, GH); Escandente, alrededores de la repressa Miraflores, *Correa 1181* (MO); Barro Colorado Island, *Croat 4400* (F, MO, SCZ); Pipeline Road at Río Agua Salud, *Croat 4731* (MO, SCZ (2)); Frijoles, near railroad station, *Croat 6265A* (MO); Barro Colorado Island, *Croat 7470* (F, MO, NY, SCZ); near Frijoles

station, *Croat* 8922 (MO, NY, SCZ), 8922 (MO, SCZ); Barro Colorado Island, *Croat* 11763 (F (2), MO), 12811 (F, MO); Pipeline Road N of Gamboa ca. 24 km beyond gate, less than 300 ft., *Croat* 38264 (MO); Barro Colorado Island, *D'Arcy* 3983 (MO); Pan-American Highway near La Chorrera, *D'Arcy* 9429 (MO); road C-21, *Duke* 5791 (MO (2), NY); Albroom, *Dwyer* 6714 (MO); Frijoles, *Ebinger* 307 (F, MEXU, MO, US); near Farfan beach, *Gentry* 1399 (F, MO, NY, SCZ); Pipeline Road, 2–4 mi. N of Gamboa, ca. 100 m, *Gentry* 6541 (C, CAS, F, L, MEXU, MO, NY, RSA); Corozal, *Greenman & Greenman* 5207 (GH, MO (2)); Gatún Station, *Hayes s.n.* (G, MO), *s.n.* (GH (2), MO, US), 608 (MO, NY (2), US); *Heriberto* 49 (NY, US); Barro Colorado Island, *Hladik* 65 (MO); Pipeline Road near Río Agua Salud, *Kennedy & Redemsky-Young* 1809 (C, F, MO, NY, US); Barro Colorado Island, *Kenoyer* 410, 641 (US); Gamboa, *McDaniel* 5045 (MO); Curundu, 30–40 m, *Miller* 1046 (MO); Gatún, *Ostenfeld* 81 (C); near old Fort Lorenzo, mouth of Río Chagres, *Piper* 5938, 5967, 5988 (US); vicinity of Ancon, *Piper* 6030 (US); between Corozal and Ancon, 10–30 m, *Pittier* 2171 (NY, US); grounds of Fort San Lorenzo, *Porter et al.* 5006 (MO, SCZ, UC); W slope of Ancon Hill, vicinity of Balboa, 20–75 m, *Seibert* 403 (MO, NY, US); Barro Colorado Island, *Shattuck* 42 (F, GH, MO), 480 (F, MO (2)), 1073 (F, MO (2)); Balboa, *Standley* 25570, 25591 (US); Summit, *Standley* 26954 (US); Balboa, *Standley* 27008 (US); Hills W of the Canal, near Gatún, *Standley* 27183 (US); Gamboa, *Standley* 28534 (US); along the old Las Cruces Trail, between Fort Clayton and Corozal, *Standley* 29114 (US); vicinity of Summit, *Standley* 29998 (US); vicinity of Fort Sherman, *Standley* 31060 (US); Obispo, *Standley* 31785 (US); Miraflores Locks area, *Tyson* 1134 (MO, SCZ); 1 mi. N of summit on road to FAA radar tower, *Tyson et al.* 2773 (MO, SCZ); Fort San Lorenzo, *Tyson & Blum* 3792 (MO); vicinity of Miraflores Lake, *White* 166 (MO, NY); north side of canal beyond bridge, *White* 91 (F, MO); vicinity of Miraflores Lake, *White* 245 (MO, NY); 1 mi. SW of Cocoli in the Rodman Naval Ammunition Depot, *Wilbur et al.* 12914 (F, LL, MEXU, MICH, NY); Barro Colorado Island, *Woodworth & Vestal* 441 (F, GH), 444 (MO), 519 (F, MO). CHIRIQUÍ: Bajo Mono-Robalo Trail, western slopes of Cerro Horqueta, 500–1,000 ft., *Allen* 4781 (MO); Cerro Colorado, 1,400 m, *Antonio* 1417 (MO); Boquete–Palo Alto–Arco Iris, *Beliz* 169 (MO); Finca Collins, vicinity of Boquete, *Blum & Dwyer* 2525A (MO, SCZ (2)); Dist. San Felix, corregimiento of Hato Culantro, Hamlet of Cerro Otoe, 3,000 ft., *Bort* 2 (MO); Burica Peninsula, San Bartolo Limite, 19 km W of Puerto Armuelles, 500 m, *Busey* 612 (MO); Chorchá, *Castillo* 3 (F, MO); camino hacia La Finca Landian, NE del campamento de Fortuna (Hornito), 1,100 m, *Correa et al.* 2355 (F, MO); Nor-oeste del campamento Fortuna, 1,000–1,200 m, *Correa et al.* 2590 (MO), 2619 (F, MO); NE del campamento de Fortuna (Hornito), 1,000–1,200 m, *Correa et al.* 2882 (MO); trail north of Cerro Punta, *Croat* 10499 (MO); between Bambito and Cerro Punta, *Croat* 10672 (MO); along the Río Chiriquí Viejo just above Guadalupe, *Croat* 16045 (F, LL, MO, NY); Burica Peninsula, 10–11 mi. W of Puerto Armuelles in vicinity of San Bartolo Limite, 300–500 m, *Croat* 22018 (F, L, LL, MO, NY, US); Burica Peninsula, Distrito Barú, along ridge above Brazo Seco near Costa Rican border, 100–200 m, *Croat* 22566 (MO); Methodist youth camp between Nueva Swissa and Cerro Punta, *Croat* 26256 (MO, NY, US); in and along wooded slopes on Cerro Horqueta, 1,650 m, *Croat* 26999 (MO); along continental divide on Cerro Colorado, on upper mining road 20–28 mi. from San Felix, 1,200–1,500 m, *Croat* 33379 (MO); Cerro Colorado, along road to copper mine, 34.1 km beyond bridge over Río San Felix near town of San Felix, 13.1 km beyond turnoff to Escopeta, 1,390 m, *Croat* 37312 (MO); Boquete, *D'Arcy & D'Arcy* 6354 (MO (2), US); Boquete District, Chiquero, *Davidson* 557 (F, MO, US); Cerro Horqueta, 1,500 m, *Duke et al.* 13628 (MO, SCZ); NW of Boquete, Cerro Horqueta, 5,000–5,800 ft., *Dwyer et al.* 537 (MO, UC, US); Tole vicinity of Santa Ana Well, ca. 1,000 ft., *Dwyer & Kirkbride* 7453 (MO, UC); Boquete, Cerro Horqueta, 5,000–6,000 ft., *Dwyer & Hayden* 7692 (MO, UC); Boquete, 7,000 ft., *Ebinger* 705 (F, MO); road from Volcán to Río Serano, road that turns eastward 7.2 km from Río Serano, 3.2 km along the side of the road, *Folsom* 4032 (MO); Boquete region, Cerro Horqueta, *Hagen & Hagen* 2072 (NY); 3.5 mi. NE of Boquete, end of road along Río Palo Alto, *Hammel* 5753 (MO); Palo Alto, 4.5 mi. NE of Boquete, 6,000 ft., *Hammel* 7478 (MO); NW of Boquete, 1,350–1,680 m, *Huft* 1812 (MO); Burica Peninsula, forest along quebradas and adjacent pastures, Quebrada Merida, 4 mi. S of Puerto Armuelles, 0–100 m, *Liesner* 397 (F, MO); upland forest 5.2 mi. NW of El Hato del Volcán on the road to Costa Rica, 5,500 ft., *Luteyn* 832 (MO); Guadalupe, 1.5 km N of Cerro Punta, *Mori & Kallunki* 5718 (MO); Dos Lagunas, 4 km W of El Hato del Volcán, 1,300 m, *Mori & Bolten* 7395 (MO); Cerro Vaca, 900–1,136 m, *Pittier* 5311 (NY, US); along the Quiel road 12.2 km above Boquete, 5,500 ft., *Proctor* 31842 (LL); Boquete, Palo Alto, just E of Boquete, 5,000 ft., *Stern et al.* 1088 (GH, MO, US); SE slopes of Cerro Pate Macho, trail from Río Palo Alto, 4 km NE of Boquete, 1,500–1,700 m, *Sytsma et al.* 4811 (MO); 6 mi. W of David, *Tyson* 924 (MO, RSA); Bambito, 1 mi. SW of Cerro Punta, 5,600 ft., *Tyson* 5661 (MO, SCZ); Dist. Boquete, above Jarimillo Arriba, along N slopes of Cerro Palo Alto, *Webster* 16687 (MO); wooded slopes and thicketed trailside along the trail between Cerro Punta and the Quebrada Bajo Grande, 2,000–2,100 m, *Wilbur et al.* 11908 (DS, F, LL, MICH, MO, NY, US); valley of the Río Chiriquí Viejo E of Guadalupe, *Wilbur et al.* 13026 (F, LL, MICH, MO, NY); Finca Lerida to Pena Blanca, 1,750–2,000 m, *Woodson & Schery* 314 (MO); vicinity of Bajo Chorro, 1,900 m, *Woodson & Schery* 613 (MO); vicinity of Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al.* 912 (MO, NY (2)). COCLÉ: El Valle de Antón, trails near Finca Tomas Arias, 600 m, *Allen* 4232 (F, MO); El Valle, back of Club Campestre, *Dwyer* 10511 (MO (2)); W of Río Guías, *Gentry* 5844 (MO); 46 km N of Penonome on road to Coclesito, 100 ft., *Hammel* 1702 (MO); El Valle de Antón, 1,000–2,000 ft., *Lewis et al.* 2575 (MO, UC); Boca del Toabre at confluence of Río Toabre and Río Coclé del Norte, *Lewis et al.* 5498 (MO, SCZ, UC); foot of Cerro Pilón, above El Valle de Antón, 2,000 ft., *Porter et al.* 4364 (MO); foot of Cerro Pilón, above El Valle de Antón, 2,000 ft., *Porter et al.* 4620 (MO, SCZ), 4656 (MO, UC); El Valle de Antón, narrow valley behind hotel Pan Americana, *Wilbur & Luteyn* 11714 (F, LL, MICH, MO, NY, RSA, US). COLÓN: vicinity of Portobelo, *Croat* 33573 (MO); along Río Iguanita

near bridge along Portobelo road, *Croat* 49776 (MO); Monkey Hill near Colón, *Lehmann* 996 (US); between France Field and Catival, *Standley* 30320 (US); between France Field, Canal Zone, and Catival, province of Colón, *Standley* 30376 (US); along roadside between 5–7 mi. SW of Portobelo towards María Chiquita, *Wilbur & Weaver* 11175 (F, GH (2), MICH, MO). DARIÉN: on hills above west end of airstrip at Caña near Río Caña, *Croat* 38073 (MO); along Río Pirre, *Duke* 4974 (MO, NY); wooded ridge just S of El Real, *Duke* 5051 (MO); Río Balsa between N. Q. Chusomocatre and Río Areti, *Duke* 8706 (MO); Isla Casaya, *Duke* 10385 (MO); 0.5–1.5 mi. E of Manene, *Hartman* 12102 (MO); El Real, trail to Río Pirre, *Kennedy* 2817 (MO); Manene to mouth of Río Cuasi, *Kirkbride & Bristan* 1417 (MO, NY). HERRERA: 11 mi. S of Ocú on Las Minas Road, *Graham* 240 (GH, MICH). PANAMÁ: vicinity of Pacora, 35 m, *Allen* 1010 (F, MO, US); San José Island, *Anderson s.n.* (GH); weedy area S of Tocumen Airport, *D'Arcy* 9643 (MO); Río Pacora just below confluence with Río Corso, *Duke* 12009 (MO); Tocumen, *Dwyer s.n.* (MO), 4225 (MO); San José Island, *Erlanson* 47 (US), 59 (G, NY), 191 (US); *Harlow* 96 (US); *Johnston* 120 (GH, US), 592, 907, 980 (GH), 1325 (GH (2)); Perlas Islands, S tip of Isla Del Rey, Punta de Cocos, 0–20 m, *Knapp & Mallet* 2911 (MO); upper slopes of Cerro Campana, *LeDoux* 2631 (MO); Chiman, *Lewis et al.* 3364 (MO); Altos de Campana, unos 35 m del Motel Sulin, 3,045 ft., *Mendez* 83 (F, MO); near Bejuca, *G. S. Miller* 1809 (US); San José Island, *G. S. Miller* 1914 (US); Sabanas, N of Panama City, *Paul* 563 (MICH, US); Punta Paitilla, *Piper* 5403, 5432 (US); Las Sabanas, *Riley* 117 (MO, US); *Standley* 25869 (US); near the big swamp E of Río Tocumen, *Standley* 26602 (US); vicinity of Juan Franco Race Track, *Standley* 27721 (US); Río Tocumen, *Standley* 29483 (US); between Las Sabanas and Matias Hernández, *Standley* 31812 (US); between Matias Hernández and Juan Diaz, *Standley* 32037 (US); road from Cerro Azul to Cerro Jefe, 2,300 ft., *Tyson* 6173 (F); La Chorrera, Las Mendozas, quebrada cerca del campo de Juegos, *Vergara & Torres* 81 (MEXU); Cerro Azul, *Viquezol* 34 (MO); thickets and forests near Arraijan, 15 m, *Woodson et al.* 1357 (F, MO, NY). SAN BLAS: hills SE of Puerto Obaldía, *Croat* 16703 (MO, NY); Mulatupu, Río Ibedi, *Duke* 8479 (MO); Sasardi, 20 m, *Duke* 10144 (MO); along canal just N of Mandinga Airport, *Duke* 14846 (MO); along headwaters of Río Mulatupu, *Elias* 1739 (MO); mountains above Puerto Obaldía, *Gentry* 1479 (MO); mainland opposite Playón Chico, 0–3 mi. from Caribbean, 0–200 m, *Gentry* 6400 (MO); mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi. inland, *Lewis et al.* 165 (MO, US); along Río Ailigandi, 0–100 ft., *Warner* 182 (MO). VERAGUAS: hills W of Sona, 500 m, *Allen* 1044 (MO, NY, US); Isla de Coiba, near María River, across bay from Colonia Penal, *Antonio* 2327 (MO); S of Santa Fe, *Nee* 8014 (MEXU, MO, RSA, US); 2 km NW of Atalaya, 100 m, *Nee* 8200 (MO); La Mesa, *Tyson* 6070 (MO, SCZ).

Cordia tacarcunensis James S. Miller, sp. nov. TYPE: Panama. Darién: trail from Pucuro to Cerro Mali, vicinity of Tapaliza River, 100 m, tropical moist for-

est, 13 Jan. 1975, *Alwyn H. Gentry & Scott Mori* 13546 (holotype, MO 2288082). Figure 5.

Arbor vel frutex ad 3 m alta, ramunculo glabro. Folia persistentia, petiolis 6–10 mm longis; laminae anguste ovato-ellipticae, 8.1–14.5 cm longae, 4.5–6.5 cm latae, apice acuminatis, base acutis, superficie papillosa. Inflorescentiae axillares, parvae dichotome cymosae, 4–6 cm latae. Flores unisexuales, plantis dioeciis; calyx campanulatus, 2.7–3 mm longus, 5-lobatus, strigillosus; corolla alba, tubuliformis, 4.8 mm longa, 5-lobata, lobo reflexa, oblonga, 2.2 mm longa; stamina 5, filis villosis, antheris ellipticis. Fructus drupaceus, putamine inaequilateraliter ovoideo, 5 mm longo.

Small tree or shrub 3 m tall, the twigs glabrous. Leaves persistent; petioles 6–10 mm long, canaliculate adaxially, minutely strigillose; blades narrowly elliptic-ovate, 8.1–14.5 cm long, 4.5–6.5 cm wide, the apex acuminate, the base acute and sometimes slightly decurrent, the margin entire, the adaxial surface lacking hairs but densely covered with small scaly papillae, the abaxial surface nearly glabrous, with small scaly papillae and a few widely scattered appressed hairs. Inflorescences axillary, numerous per stem, dichotomous cymes, 4–6 cm broad, the axes densely brown strigillose. Flowers unisexual, the plants dioecious. Female flowers with small, nonfunctional anthers, sessile; calyx campanulate, 2.7–3 mm long, 3–3.5 mm wide at mouth, ribs absent, dark-brown strigillose, the 5 lobes shallowly triangular, 0.5 mm long; corolla white, tubular with reflexed lobes, 4.8 mm long, 5-merous, the lobes oblong, 2.2 mm long, 1 mm wide, the tube 2 mm long; stamens 5, nonfunctional, the filaments 2.8 mm long, the upper 2 mm free, villous toward the middle of the free portion, the anthers ellipsoid, 0.5 mm long; ovary ovoid, 2.3 mm long, 2 mm broad; disc crateriform, 0.4 mm tall, 1.2 mm broad, glabrous; style 2.5 mm long, the stylar branches 1.9 mm long, the stigma lobes fan-shaped. Male flowers unknown. Fruits seated in the slightly accrescent saucer-shaped calyx, drupaceous, glabrous, the stone inequilaterally broadly ovoid, 5 mm long, 5 mm broad, endocarp bony, 1-seeded.

Distribution. *Cordia tacarcunensis* is known only from the type collection made

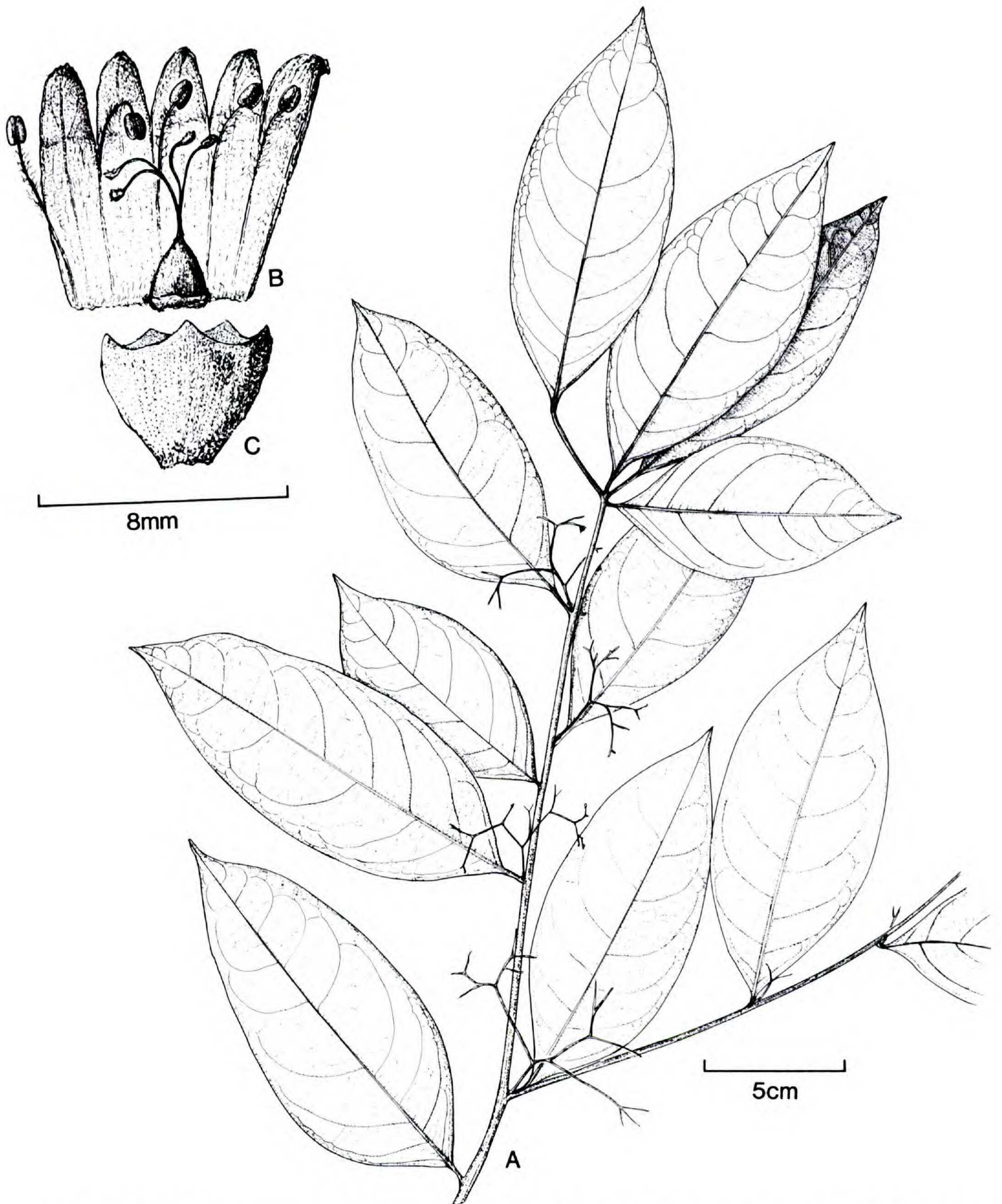


FIGURE 5. *Cordia tacarcunensis*.—A. Flowering branch.—B. flower with corolla opened.—C. Calyx. From Gentry & Mori 13546 (MO), Darién, Panama.

near the base of Cerro Tacarcuna on the Colombia–Darién border.

Cordia tacarcunensis is probably most closely related to *C. protracta* and *C. correae*, with which it shares a similar growth

habit and a three-parted calyx. It is distinctive, however, in its small, axillary inflorescences and its fan-shaped stigma lobes. In addition to the *C. panamensis* and *C. diversifolia* species groups, *C. tacarcunensis* is the only member of sect. *Myxa* in Central

America known to be dioecious; the breeding systems of its two presumed closest relatives are not known.

Cynoglossum L., Sp. Pl. 134. 1753; Gen. Pl. ed. 5. 65. 1754. TYPE: *Cynoglossum officinale* L., vide Britton & A. Brown, Ill. Fl. N. U.S. ed. 2, 3: 75. 1913.

Perennial (rarely annual or biennial) herbs from a thickened rootstock, usually branched, pubescent or rarely glabrous. Leaves alternate, simple, entire, the basal leaves on distinct petioles, the cauline leaves usually sessile. Inflorescences racemes or panicles, the branches scorpioid, usually ebracteate. Flowers bisexual, usually pedicellate; sepals 5, nearly distinct to the base, accrescent in fruit; corolla blue, purple, or rarely white, salverform to campanulate, 5-lobed, with 5 apparent protuberances in the mouth; stamens 5, the anthers on short filaments or nearly sessile, oblong to ellipsoid; ovary 4-lobed, the style gynobasic, the stigma 1, capitate. Fruits of 4 spreading nutlets, attached apically to the gynobase, the scar restricted to the apical half of the ventral surface, the dorsal surface with short glochidiate spines.

Cynoglossum contains about 80 species found throughout much of the world although generally absent from lowland tropical forest. Many species are cultivated ornamentals and this, combined with the epizoochorously dispersed, glochidiate spiny fruits, has allowed many members of the genus to become naturalized far from their natural ranges.

Cynoglossum amabile Stapf & J. R. Drumm., Kew Bull. 1906: 202. 1906. SYNTYPES: China. Yunnan: Mengtze, *W. Hancock* 133 (K, not seen); Szemao, 350 m, *A. Henry* 9365 (MO). Sichuan: Tatsienlu, *Soulié* 861 (K, not seen); without locality, 2,700–4,050 m, *A. E. Pratt* 887 (K, not seen); without locality, *M. Leichtlin* s.n. (K, not seen).

Erect biennial or perennial herb from a thick rootstock, to 0.5(–1) m tall, the stems

densely strigose. Basal leaves on petioles to 4.5(–11) cm long, the blade narrowly elliptic, 6–11(–17) cm long, (1–)1.5–2.5(–3) cm wide, the apex acute, the base attenuate to cuneate, the margin entire, the adaxial surface strigillose to strigose, the abaxial surface pilose to pubescent; cauline leaves sessile, lanceolate to narrowly elliptic, 3–6(–8) cm long, 0.7–2 cm wide, the apex acute, the base clasping and usually somewhat lobed, the margin entire, the adaxial surface strigillose to strigose, the abaxial surface pubescent to hirtellous. Inflorescence terminal, a panicle of small cymes, to 16(–30) cm long, the branches cymose, densely strigillose. Flowers bisexual, on pedicels to 5 mm long; sepals 5(–7), lanceolate to lance-ovate, 2–3(–4) mm long, strigose; corolla blue, rotate, 5(–7)-merous, the lobes widely obovate, 2–3(–4) mm long, the tube 1.3–2.5 mm long, with 5 hooded protuberances in the mouth, these alternate with the stamens and often puberulent; stamens 5(–7), the anthers ellipsoid, (0.5–) 0.8–1.3 mm long, nearly sessile or on short filaments to 0.5 mm long, inserted just below the mouth of the corolla tube; ovary 4-lobed, the surface smooth, the disc basal, the style gynobasic, 0.8–2 mm long, the stigma capitate. Fruits of 4 spreading nutlets, 4–6 mm broad, the nutlets ovate, flat to convex on the dorsal surface, with glochidiate spines to 0.5 mm long.

Distribution. *Cynoglossum amabile* is native to China but has become commonly naturalized in the Neotropics, being found in open areas at elevations above 1,500 m in elevation. In Panama, it is known only from Chiriquí; it is undoubtedly also in adjacent parts of Bocas del Toro.

Cynoglossum amabile can be easily distinguished from *Hackelia mexicana* (Schldl. & Cham.) I. M. Johnston, the other common small blue-flowered species of Boraginaceae in Chiriquí, by the shorter spines on its fruits and the cauline leaves usually clasping at the base, rather than cuneate as in *H. mexicana*. The only one of the syntypes that I have seen

is the collection made by A. Henry, which is labeled as having pink flowers. As blue flowers are characteristic of the species and pink-flowered forms are unusual, the selection of a lectotype will have to be from one of the remaining specimens.

Additional specimens examined. PANAMA. CHIRIQUÍ: Dist. of Boquete, E of Cerro Punta, area called Bajo Chorro, 2,600 m, *Antonio 1032* (MO); Monte Azul, 1.4 mi. N of Entre Ríos on E slopes of Cerro Punta, 3 mi. by road from town of Cerro Punta, 2,250 m, *Antonio 2723* (MO); Cerro Punta-David, 1,000-2,500 m, *Beliz 218* (MO); Volcán Barú, 3,474 m, *Beliz 355* (MO); Finca Collins, vicinity of Boquete, *Blum & Dwyer 2580* (MO); 5.4 km del Hato de Volcán en el camino a Las Lagunas, *Correa & Lazor 1472* (MO); 2 mi. N of El Hato del Volcán, *Croat 10466* (MO (2)); roadside between Bambito and Cerro Punta, *Croat 10592* (MO); roadsides between Cerro Punta and Bajo Grande, *Croat & Porter 16003* (MO); along the Río Chiriquí Viejo just above Guadalupe, *Croat & Porter 16053* (MO); E of Boquete along forested slopes and pastures on Cerro Azul near Quebrada Jaramillo, 1,500-1,620 m, *Croat 26779* (MO); 10 mi. above Boquete on road to Volcán Barú, 2,600 m, *Croat 34828, 34829* (MO); across river from town of Cerro Punta, *D'Arcy & D'Arcy 6528* (MO); Alto Respinga, 2,750 m, *D'Arcy 12158* (MO); E slope of Volcán de Chiriquí (Barú) WNW of Boquete, 2,200-2,300 m, *Davidse & D'Arcy 10173* (MO); Cerro Horqueta, 1,500 m, *Duke et al. 13608* (MO); NW of Boquete, Cerro Horqueta, 5,000-5,800 ft., *Dwyer et al. 443* (GH, MO); Boquete, Finca Collins, 5,000 ft., *Dwyer & Hayden 7650* (MO); Cerro Horqueta, 4,500-5,000 ft., *Dwyer & Tallallum 8748* (MO); above Cerro Punta, 6,500 ft., *Folsom et al. 2039* (MO); along Boquete trail, Cerro Respinga, E of town of Cerro Punta, 2,000-2,500 m, *Gentry 5931* (GH, MO); path above Cerro Punta to Boquete, 2,500 m, *Hamilton & Stockwell 3345, 3420* (MO); *Hamilton & Krager 3739* (MO); hill E of Audobon Cabin, S of Cerro Punta, 1,400-1,800 m, *Hamilton & Krager 3870* (MO); Bajo Chorro, *Hladik 183* (MO); Finca Collins, 6,000 ft., *Kirkbride 128* (MO (2)); vicinity of Las Nubes, 2.7 mi. NW of Río Chiriquí Viejo W of Cerro Punta, 2,200 m, *Liesner 290* (MO); N end of town of Cerro Punta, *Mori & Kallunki 5626* (MO); Bajo Grande, ca. 3 km E of town of Cerro Punta, 2,200 m, *Nee 9952* (MO); vicinity of Cerro Punta, 6,800 ft., *Ridgway & Solis 2396* (MO); Volcán Barú, E slope along road to Boquete, 8 km W of Boquete, 2,200 m, *Stein 1282* (MO); vicinity of Boquete, Finca Collins, 5,500 ft., *Stern et al. 1097* (GH, MO); vicinity of Boquete, Finca Collins, "El Velo," 6,150 ft., *Stern et al. 1962* (MO); 3.7 km E of bridge NE of Cerro Punta on road through Bajo Grande, 2,250-2,400 m, *Stevens 18150* (MO); 3.7 km along road through Bajo Grande from bridge NE of Cerro Punta, 2,250-2,400 m, *Sytma & Stevens 2155* (MO); Bambito, 1 mi. SW of Cerro Punta, 5,600 ft., *Tyson 5623* (MO); above Cerro Punta toward Bajo Grande in Quebrada Bajo Grande, 6,500 ft., *Wilbur et al. 10909* (MO); vicinity of Bajo Mono and Quebrada Chiquero, 1,500 m, *Woodson & Schery 523* (GH (2), MO).

Ehretia P. Browne, Civ. Nat. Hist. Jamaica 168. 1756. TYPE: *Ehretia tinifolia* L., Syst. Nat., ed. 10. 936. 1759.

Trees or shrubs, pubescent or glabrous. Leaves alternate, petiolate, entire or serrate. Inflorescences terminal, cymose to paniculate. Flowers bisexual; sepals 5, imbricate or open in bud; corolla white, tubular with 5 spreading lobes; stamens 5, usually exerted, the lower portion of the filaments adnate to the corolla tube, the anthers oblong to ellipsoid; ovary ovoid, 2- or 4-locular, the style terminal, bifid, the stigmas 2, clavate or capitate. Fruits drupaceous, ovoid to nearly spherical, the stone separating into 2, 2-seeded or 4, 1-seeded pyrenes.

The pantropical genus *Ehretia* comprises about 50 species with most occurring in Africa and tropical Asia. Only three species are known from the New World, one of which is found in Panama.

Ehretia latifolia DC., Prodr. 9: 503. 1845. TYPE: Herb. Amat. (holotype, G-DC, not seen; microfiche, MO).

Ehretia mexicana S. Watson, Proc. Amer. Acad. Arts 26: 144. 1891. TYPE: Mexico. Jalisco: base of mountains near Lake Chapala, *C. G. Pringle 3085* (lectotype, here designated, GH; isolectotypes, BH, BM, F, GH, MO, NY (2), UC, US (2)).

Ehretia luxiana J. D. Smith, Bot. Gaz. (Crawfordsville) 18: 5. 1893 (corrected reprint). TYPE: Guatemala. Quiche: San Miguel Uspantán, 6,100 ft., Apr. 1892, *Heyde & Lux 3065* (holotype, F 575900; isotypes, MO, NY, US).

Ehretia cordifolia Robinson, Proc. Amer. Acad. Arts 29: 319. 1894. TYPE: Mexico. Jalisco: valley, Zapotlán, 19 May 1893, *C. G. Pringle 4382* (holotype, F 106011; isotypes, A, BM, GH, MO, NY, UC, US (2)).

Ehretia viscosa Fern. in Sarg., Trees & Shrubs 1: 25, pl. 13. 1902. TYPE: Mexico: Morelos, near Cuernavaca, 29 May 1899, *C. G. Pringle 7777* (holotype, F 120287; isotypes, BH, GH, MEXU (2), MO, NY, UC).

Ehretia tehuacana Greenman, Publ. Field Columbian Mus., Bot. Ser. 2: 339. 1912. TYPE: Mexico. Puebla: Las Mohoneras, Tehuacán, 2,200 m, *C. Conzatti 2220* (holotype, F 235156; isotype, GH).

Ehretia austin-smithii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 984. 1938. TYPE: Costa Rica. Alajuela: Zarcero, in pasture, 1,850 m, Mar. 1938, *Austin Smith H528* (holotype, F 919653; isotype, MO).

Tree to 10 m tall, the twigs glabrous or nearly so. Leaves persistent; petioles 7–18 mm long, glabrous or nearly so; blades ovate, 4–13 mm long, 2–6.6 cm wide, the apex acute to slightly acuminate, the base obtuse to rounded, the margin serrate, the adaxial surface glabrous to sparsely strigillose, the abaxial surface glabrous. Inflorescence terminal, paniculate, to 8 cm long and 7 cm broad, the peduncle glabrous to sparsely puberulent. Flowers sessile, bisexual; sepals 5, ovate to narrowly triangular, 1.5–2 mm long, ciliate along the margin but otherwise glabrous; corolla white, 5-merous, the lobes ovate, 1.5–2.8 mm long; stamens 5, the filaments 4.5–5 mm long, the upper 3.4–4.4 mm free, glabrous, the anthers ellipsoid, 1–1.5 mm long; ovary broadly ovoid, 1–1.5 mm long, the style bifid, 1.4–3.3 mm long, the stigma lobes truncate. Fruits drupaceous, white, ellipsoid to ovoid, 10–15 mm long.

Distribution. *Ehretia latifolia* is known from Mexico south to Chiriquí Province in Panama, where it is found at 1,000–2,500 m in elevation.

Ehretia latifolia, as here defined, is a widespread, variable species. The numerous synonyms are based on minor variations in leaf shape and indument, characters that vary considerably on an individual tree as well as between individuals of a single population (Miller, unpubl.). As in most species of *Ehretia*, the plants are quite attractive while in flower, but flowering occurs only for a short period.

Additional specimens examined. PANAMA. CHIRIQUÍ: a lo largo del camino que va de Bambito a los llanos de lava, 6,000 ft., *Correa & Lazor 1410* (F, MO); at opening to canyon to Bambito, 5,000 ft., *Tyson 5870* (MO (2)); Río Chiriquí Viejo Valley, near Bambito, *White 220* (F, GH, MO).

Hackelia Opiz in Bercht., Oekon.-techn. Fl. Böhm. 2(2): 146. 1838. TYPE: *Hackelia deflexa* (Wahlenb.) Opiz in Bercht., Oekon.-techn. Fl. Böhm. 2, pt. 2, 147. 1839; I. M. Johnston, Contr. Gray Herb. 68: 45. 1923.

Erect, perennial or biennial herbs, pubescent or less commonly glabrous. Leaves alternate, entire, the basal leaves usually long-petiolate, the cauline leaves short-petiolate to sessile. Inflorescence a raceme or panicle, the branches scorpioid, ebracteate or with inconspicuous bracts. Flowers bisexual; sepals 5, free to the base or nearly so, slightly accrescent in fruit; corolla blue, often with a yellow center, or rarely white to pale yellow, salverform, 5-lobed, with 5 well-developed protuberances in the mouth; stamens 5, included in the corolla tube, the anthers elliptic to oblong, on short filaments; ovary 4-lobed, the style gynobasic, the stigma capitate. Fruits of 4 nutlets, the attachment to the pyramidal gynobase medial, the scar conspicuous, the dorsal surface with elongate glochidiate spines, these longer along the margins.

Hackelia is a genus of about 40 species of the New World, Europe, and Asia; it is clearly centered in western North America. Only a single species occurs in Panama.

Hackelia mexicana (Schldl. & Cham.) I. M. Johnston, Contr. Gray Herb. 68: 46. 1923. *Cynoglossum mexicanum* Schldl. & Cham., Linnaea 5: 114. 1830. *Echinosperrum mexicanum* (Schldl. & Cham.) Hemsley, Biol. Cent.-Amer., Bot. 2: 377. 1882. *Lappula mexicanum* (Schldl. & Cham.) E. Greene, Pittonia 2: 1882. 1891. TYPE: Mexico. Veracruz: in Monte Macuiltepetl, near Jalapa, *Schiede 208* (not seen).

Lappula costaricensis Brand in Fedde, Repert. Spec. Nov. Regni Veg. 18: 310. 1922. *Hackelia costaricensis* (Brand) I. M. Johnston, Contr. Gray Herb. 68: 46. 1923. TYPE: Costa Rica: San José, *Hoffman 152* (not seen).

Lappula guatemalensis Brand in Fedde, Repert. Spec. Nov. Regni Veg. 18: 311. 1922. *Hackelia guatemalensis* Brand in Engl., Pflanzenr. 4, 252: 120. 1931. SYNTYPES: Guatemala: Quiche, *Heyde & Lux 3043* (not seen). Guatemala: Huehuetenango, *Seler & Seler 3144* (not seen).

Erect perennial herb from a thick rootstock, to 1.5 m tall, the stems pubescent. Basal leaves on petioles 9–17 cm long, lanceolate, 6–15 cm long, 2.5–4.5 cm wide, the

apex acuminate to attenuate, the base cuneate to decurrent, the margin entire, cauline leaves lanceolate to elliptic, 8–23 cm long, 2–7.5 cm wide, the apex acuminate, the base cuneate to decurrent, the margin entire, the uppermost usually sessile, those below on petioles to 16 cm long, the adaxial surface strigose, the abaxial surface strigose to sparsely pilose, densely strigose along the main veins. Inflorescences terminal or from the upper leaf axils, a simple or once-branched raceme, 12–25 cm long, the rachis strigose to hirsute. Flowers bisexual, on pedicels to 5 mm long, these elongating to 15 mm in fruit; sepals 5, lanceolate, 1.5–2 mm long, strigose; corolla blue, yellow in the mouth, rotate, 5-merous, the lobes very widely ovate or obovate to widely oblong, 1.5–2.5 mm long, the tube 1.4–2 mm long, with 5 protuberances in the mouth; stamens 5, the anthers ellipsoid, 0.5–0.7 mm long, nearly sessile, inserted in the middle of the corolla tube; ovary 4-lobed, the lobes tuberculate, enclosed at the base by the disc, the style gynobasic, 0.5–0.7 mm long, the stigma capitate. Fruits of 4 nutlets, 2.5–3.2 mm long, densely glochidiate, the spines 1–4 mm long.

Distribution. *Hackelia mexicana* occurs from Mexico, south through Central America, to Venezuela, Colombia, Ecuador, and Peru, where it can be found in open disturbed areas at 1,200–3,500 m in elevation. In Panama, it is known only from upland Chiriquí, but it is certainly expected in adjacent areas of Bocas del Toro.

Hackelia mexicana is a common weed of upland Chiriquí, where it is highly visible and distinct with its bright blue flowers. In this region *H. mexicana* is most easily confused with *Cynoglossum amabile*, although, as indicated under the latter species, *H. mexicana* differs in having cauline leaves that are not clasping at the base, nutlets with a medial attachment to the gynobase, and much longer glochidiate spines on the nutlets.

Additional specimens examined. PANAMA. CHIRIQUÍ: E of Cerro Punta, area called Bajo Chorro, 2,600 m, *Antonio 1023* (MO); Cerro Punta, 7,000 ft., *Blum et*

al. 2422 (MO); slopes of Las Cumbres near Cerro Punta, *Croat 13679* (MO); Las Cumbres, hogback ridge N of Quebrada Iglesia, near town of Cerro Punta, *Croat & Porter 16096* (MO); 12 mi. above Boquete on road to Volcán Barú, 2,900–2,950 m, *Croat 34900* (MO); E slope of Volcán de Chiriquí (Barú), above Boquete, *Davidse & D'Arcy 10284* (MO); Potrero Muleto, Volcán de Chiriquí, 10,400 ft., *Davidson 1018* (GH, MO); just below last climb in Alto Respinga, 2,700 m, *D'Arcy 12135* (MO); Alto Respinga and above, 2,800 m, *D'Arcy s.n.* (MO); along Boquete Trail, Cerro Respinga, 2,000–2,500 m, E of town of Cerro Punta, *Gentry 5949* (GH, MO); along Boquete trail, Cerro Respinga, 2,000–2,500 m, E of town of Cerro Punta, *Gentry 6014* (MO); path above Cerro Punta to Boquete, 2,500 m, *Hamilton & Stockwell 3421* (MO); path above Cerro Punta to Boquete, 2,500 m, *Hamilton & Krager 3738* (MO); Bajo Chorro, *Hladik 195* (MO); near Paso de Respingo, in pasture and disturbed oak forest, ca. 2,300 m, *Mori & Kallunki 5737* (MO); around El Potrero camp, 2,800–3,000 m, *Pittier 3106* (GH); vicinity of Cerro Punta, 6,800 ft., *Ridgway & Solis 2394* (MO); ca. 3.7 km E of bridge NE of Cerro Punta on road through Bajo Grande, 2,250–2,400 m, *Stevens 18217* (MO); 3.7 km along road through Bajo Grande from bridge NE of Cerro Punta, 2,250–2,400 m, *Sytsma & Stevens 2117* (MO); along the trail between Cerro Punta and the Quebrada Bajo Grande, 2,000–2,100 m, *Wilbur et al. 11897* (GH); Finca Lerida to Peña Blanca, 1,750–2,000 m, *Woodson & Schery 333* (GH (2), MO); vicinity of Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al. 890* (GH (2), MO).

Heliotropium L., Sp. Pl. 130. 1753; Gen. Pl. ed. 5, 130. 1754. TYPE: *Heliotropium europeum* L., Sp. Pl. 130. 1753.

Annual or perennial herbs or rarely low shrubs. Leaves alternate, rarely opposite or whorled. Inflorescences bracteate or ebracteate, helicoid cymes borne singly or in groups of 2–4, or the flowers borne individually along leafy stems. Flowers bisexual; sepals 5, imbricate, free or nearly so to the base, often unequal in size, occasionally accrescent; corolla salverform, funnelform, or tubular, white, or white with a yellow center, or occasionally blue to purple, 5-lobed; stamens 5, inserted in the throat of the corolla tube, the anthers free or apically connate; ovary 4-locular, often 4-lobed, the style terminal or absent, the stigma 1, conical. Fruits dry, breaking into 2 or 4 nutlets at maturity.

Heliotropium comprises about 200 species and is essentially cosmopolitan, with the greatest number of species occurring in dry, tropical regions. Despite the relative abun-

dance of species in most neotropical countries, only four species are known from Panama. These are all widespread, weedy species found throughout the Neotropics, and two have become widespread in the Old World. *Heliotropium arborescens* L., a South American species, is often cultivated for its attractive purple flowers and might be found in gardens in Panama, although no collections exist.

The pantropical genera *Heliotropium* and *Tournefortia* L., and the monotypic Argentine genus *Ixorhea* Fenzl make up the subfamily Heliotropioideae. *Heliotropium* is a morphologically diverse genus, and Johnston (1928) recognized 11 sections in South America, three of which are known from Panama. *Heliotropium* is a genus of herbs with dry fruits, in contrast with the woody habit and fleshy fruits that characterize *Tournefortia*.

KEY TO THE SPECIES OF *HELIOTROPIUM* IN PANAMA

- 1a. Plants glabrous *Heliotropium curassavicum*
- 1b. Plants with pubescent stems and leaves.
 - 2a. Inflorescence terminal or internodal, spicate or a helicoid cyme, with numerous flowers.
 - 3a. Corolla lavender; plants erect; leaves wider than 2 cm ... *Heliotropium indicum*
 - 3b. Corolla white; plants procumbent; leaves narrower than 2 cm
..... *Heliotropium procumbens*
 - 2b. Inflorescence axillary, 1-flowered
..... *Heliotropium lagoense*

***Heliotropium curassavicum* L., Sp. Pl. 130. 1753.** TYPE: Curaçao: *P. Browne s.n.* (holotype, LINN (Savage Catalog number 179.11), not seen; microfiche, MO).

Low herb, often somewhat succulent, glabrous, often glaucous, the stems procumbent to ascending. Leaves lacking a distinct petiole; blades oblanceolate, 10–35 mm long, 1–5(–10) mm wide, the apex acute to rounded, the base cuneate, the margin entire, glabrous and often glaucous on both surfaces. Inflorescence internodal, a once- or twice-branched helicoid cyme, rarely simple, the peduncle 11–20(–32) mm long, the branches (1.8–)3–6(–8) cm long. Flowers bisexual; sepals 5,

lanceolate to ovate or oblong, ca. 1.5 mm long, glabrous; corolla white, 2–2.5 mm long, the 5 lobes 1 mm long, the tube 1 mm long, glabrous; stamens 5, the anthers nearly sessile, inserted near the middle of the corolla tube, ellipsoid, 0.5–0.8 mm long; ovary ovoid, the disc well developed, the stigma sessile, broadly conical. Fruits ovoid, 1–2 mm long, glabrous, 4-lobed, separating into 4 nutlets at maturity.

Distribution. *Heliotropium curassavicum* is usually found growing along the edges of lakes, streams, or tidal flats from sea level to 600 m in elevation. It occurs from the United States through Central America and the West Indies and South America; it has also apparently become introduced and widespread in the Old World (Nowicke & Miller, in press). This species is known in Panama only from the province of Los Santos.

Heliotropium curassavicum is one of the most distinctive species of the genus and is the only member of sect. *Halmyrophila* I. M. Johnston. It is easily recognized by its glabrous, succulent nature. Several varieties of this species have been recognized (Johnston, 1928; Frohlich, 1981); the populations in Panama are all of the typical variety.

Additional specimens examined. PANAMA. LOS SANTOS: Salinas de Chitré, *D'Arcy & Croat 4199* (MO); Monagre Beach, *Dwyer 4177* (MO (2)); Monagre Beach, 5 mi. SE of Chitré, *Tyson et al. 3023* (MO).

***Heliotropium indicum* L., Sp. Pl. 130. 1753.** TYPE: *P. Browne s.n.* (holotype, LINN (Savage Catalog number 179.2), not seen; microfiche, MO).

Annual herb to 50 cm tall, the stems pubescent to pilose, the hairs simple. Leaves on petioles (7–)10–25(–40) mm long, pubescent, often pilose at the base; leaf blade ovate, (2.7–)5–10(–12) cm long, (2–)3–5(–7) cm wide, the apex acute to obtuse, the base obtuse to truncate and usually decurrent along the petiole, the margin unevenly serrate to undulate, the adaxial surface with widely scattered appressed hairs, the abaxial surface nearly glabrous with only a few hairs scattered

along the veins, to nearly villous. Inflorescence internodal, an unbranched or very rarely dichotomous helicoid cyme, the peduncle (1-)2-3(-6) cm long, pubescent, the fertile portion (6-)9-16(-20) cm long. Flowers bisexual; sepals 5, lanceolate, 2-3 mm long, pubescent; corolla purple to occasionally white, salverform, 5-merous, the lobes ovate, 1-1.5 mm long, the tube 3-4 mm long, pubescent outside; stamens 5, the anthers sessile or nearly so, inserted just below the middle of the corolla tube, ellipsoid, 0.6-0.8 mm long; ovary globose, 0.5-1 mm long, the disc well-developed, the style 0.5-1 mm long, the stigma capitate. Fruits angular ovoid, with an apical beak, 2-3 mm long, glabrous, the 2 lobes spread apart and ultimately separating into 2 nutlets at maturity.

Distribution. *Heliotropium indicum* is a weed of disturbed habitats from sea level to 1,000 m in elevation nearly throughout the world with the exception of cold regions. In Panama, it is known from all regions except the Comarca de San Blas, but is probably there as well.

Heliotropium indicum is a coarse, annual weed and one of the most commonly encountered species of the genus. Although it is essentially worldwide in distribution, Johnston (1928) suggested that it was probably South American, possibly Brazilian, in origin. Its closest relative is *H. elongatum* Hoffm. ex Roemer & Schultes, a species of southeastern South America, and the two make up sect. *Tiaridium* (Lehm.) Griseb., which is characterized by a weedy, annual habit, salverform corollas, and ribbed, glabrous fruits. *Heliotropium indicum* is easily recognized by its purple (rarely white) corollas and strongly angular fruits with prolonged apices.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Bocas del Toro, *Carleton 195* (GH); Old Bank Island, *Wedel 1986* (GH, MO). CANAL AREA: Pipeline Road to 18 km N of Gamboa, *D'Arcy 10618* (MO); flooded pasture bordering Chagres River, about 2 mi. N of Gamboa, *Lazor 3498* (MO); Barro Colorado Island, *Starry 249* (MO). CHIRIQUÍ: Burica Peninsula, 1 mi. W of Puerto Armuelles, 50 m, *Croat 22029* (MO); Burica Peninsula, dist. Guanabano, disturbed areas along Que-

brada Quanabano, 0-100 m, *Croat 22532* (MO); vicinity of San Bartolome, Peninsula de Burica, 0-50 m, *Woodson & Schery 925* (GH). COCLÉ: El Valle, *Aguilar 48* (MO); Río Coclé, W of Penonomé, *Folsom 2917* (MO); 12 mi. NE of Penonomé, 1,200 ft., *Lewis et al. 1524* (GH, MO); Boca del Toabre at confluence of Río Toabre and Río Coclé del Norte, *Lewis et al. 5512* (MO). COLÓN: Portobelo, 5-100 m, *Pittier 2470* (GH). DARIÉN: El Real, *Correa & Lazor 1534* (MO); El Real, Río Tuirá, *Stern et al. 452* (GH, MO). HERRERA: Roadside between El Potrero and Las Minas, *Croat 9650* (MO); just S of Ocú, *D'Arcy 4127* (MO (2)); 5 km W of turnoff from highway 105 to Potuga, *Hammel 5254* (MO); 3 km from Pesé on road to Ocú, *Huft 1734* (MO). LOS SANTOS: along road between Tonosi and Jobero, 50-80 m, *Croat 34446* (MO); 5 mi. S of Pocrí, *D'Arcy & Croat 4209B* (MO); Río Tonosi, vicinity of Tonosi, *Lewis et al. 1558* (GH, MO). PANAMÁ: Isla Taboga, 0-350 m, *Allen 1297* (GH, MO); beneath bridge on Interamerican Highway near end of Tocumen Airport runway, *Croat 9771* (MO); between Chepo and wharf, *Dodge 10721* (MO); Isla San Miguel, *Duke 10937* (MO); Bayano Guipo forest, disturbed area round lake near Bayano Bridge, *Folsom 3551* (MO); Taboga Island, *Macbride 2792* (MO); between Chepo and Río Bayano, *Porter et al. 5173* (MO); Taboga Island near village, Perlas Islands, *Tyson 5591* (MO); Río Tattare, *Woodson & Schery 995* (GH). VERAGUAS: 1.3 km E of the intersection of the Panamerican Highway and road P38 to Atlaya, *Folsom 2932* (MO); 2 mi. S of Canazas, *Tyson 3725* (MO).

Heliotropium lagoense (Warm.) Gürke in Engl. & Prantl, Nat. Pflanzenfam. 4 Abt. 3a, 97. 1893. *Schleidenia lagoensis* Warm., Vidensk. Meddel. Dansk Naturhist. Forren. Kjobenhavn 1867: 15. 1868. TYPE: Brazil. Minas Gerais: Lagoa Santa, 1863-1866, *Warming 21971* (C, holotype, not seen; photo, MO).

Procumbent herb, the stems with a few scattered, appressed hairs. Leaves on short petioles to 1.5 mm long; blade narrowly elliptic to oblanceolate, 3-6 mm long, 1.2 mm wide, the apex acute, the base acute, the margin entire, the adaxial surface glabrous, the abaxial surface glabrous or with a few scattered, appressed hairs. Flowers borne individually in the leaf axils, on pedicels 2-4 (-6) mm long; sepals 5, ovoid, ca. 2 mm long, glabrous; corolla pale blue to white and yellow in the throat, the 5 lobes widely ovate, ca. 1 mm long, the tube ca. 2 mm long, glabrous; stamens 5, the anthers ovoid, ca. 0.4 mm long, sessile, inserted near the middle of the corolla tube; ovary ovoid, ca. 0.5 mm long,

the disc scarcely evident, the stigma sessile, capitate. Fruits ovoid, 1.2 mm long, glabrous, 4-lobed, separating into 4 nutlets at maturity.

Distribution. *Heliotropium lagoense* occurs from Mexico through South America and the West Indies, and is found at elevations below 200 m (rarely to above 1,000 m) usually in open savannas. In Panama, it is known from a single collection from the province of Coclé.

Heliotropium sect. *Orthostachys* R. Br. is the largest section of the genus and certainly the most complex taxonomically. It is found throughout tropical regions of the world and is particularly well represented in the Neotropics, where Johnston (1928) suggested that approximately 50 species occur. *Heliotropium lagoense* and *H. procumbens* are the only members of the section known to occur in Panama. *Heliotropium lagoense* is a member of subsect. *Axillaria* and is easily recognized by its diminutive habit of growth and axillary flowers that are not aggregated into the helicoid cymes that characterize all of the other Panamanian species.

Additional specimens examined. PANAMA. COCLÉ: mountains beyond Pintada, 400–600 m, *Hunter & Allen 525* (MO).

Heliotropium procumbens Miller, Gard. Dict. ed. 8, no. 10. 1768; I. M. Johnston, Contr. Gray Herb. 81: 52. 1928. TYPE: Colombia. Bolívar: Cartagena, *Houston s.n.* (holotype, BM, not seen).

Heliotropium americanum Miller, Gard. Dict. ed. 8, no. 10. 1768. TYPE: Mexico. Veracruz: *Houston s.n.* (holotype, BM, not seen).

Heliotropium inundatum Sw., Prodr. 40. 1788. TYPE: Jamaica (not seen).

Heliotropium decumbens Lehm., Nov. Actorum Acad. Caes. Leop. Carol. German. Nat. Cur. 9: 128. 1818. TYPE: Venezuela. Sucre: Cumaná, *Humboldt 57* (holotype, P, not seen; microfiche, MO).

Heliotropium simplex Meyen, Reise 1: 436. 1834. TYPE: Chile. Tacna: Arica, *Meyen s.n.* (holotype, B, not seen).

Heliotropium inundatum var. *cubense* DC., Prodr. 9: 540. 1845. TYPE: Cuba. La Habana: near Havana, 1829, *Ramón de la Sagre 239* (holotype, G-DC, not seen; microfiche, MO).

Heliotropium bridgesii Rusby, Mem. Torrey Bot. Club

4: 224. 1895. TYPE: Bolivia. Cochabamba: Cochabamba, *M. Bang 950* (holotype, NY; microfiche, MO; isotype, US).

Heliotropium inundatum var. *chacoense* R. E. Fries, Ark. Bot. 6(11): 22. 1906. TYPE: Bolivia. Tarija: along Río Pilcomayo near Ft. Crevaux, *Fries 1614* (isotype, US).

Herb to 30 cm tall, the stems procumbent to ascending, strigose to pubescent. Leaves on petioles (3–)5–10(–15) mm long, strigose to pubescent; leaf blade elliptic to narrowly elliptic, 11–20(–35) mm long, 6–11(–17) mm wide, the apex acute to rounded, the base acute to cuneate, the margin entire, the adaxial surface strigose, the abaxial surface strigose to sericeous. Inflorescence internodal or terminal, a once- or twice-branched helicoid cyme, the peduncle (3–)8–20(–26) mm long, strigose to sericeous, the fertile portion 20–45(–75) mm long. Flowers bisexual; sepals 5, lanceolate, 1–1.2 mm long, one often exceeding the others in length, strigose; corolla white, the 5 lobes lanceolate to lance-ovate, 0.5–0.6 mm long, the tube 0.9–1.2 mm long, villous in mouth, strigose to strigillose outside; stamens 5, the anthers ellipsoid but acuminate at the apex, 0.2–0.3 mm long, sessile or nearly so, inserted from near the base to just beneath the middle of the corolla tube; ovary globose, 0.2–0.3 mm long, the disc scarcely evident, the stigma sessile, capitate. Fruits globose, ca. 1 mm long, strigillose, faintly 4-lobed, separating into 4 nutlets at maturity.

Distribution. *Heliotropium procumbens* is widespread from the southern United States south throughout all of the Neotropics, at elevations of 0–1,500 m in a wide variety of habitats. In Panama, it is known from the provinces of Coclé, Herrera, Los Santos, and Panamá.

A common weed, *Heliotropium procumbens* is extremely variable in shape, size, and indument of its leaves. Its wide geographic distribution and morphological variability have spawned considerable taxonomic problems, and numerous segregates have been proposed. Despite this, the species has been interpreted broadly by most recent authors.

Additional specimens examined. PANAMA. COCLÉ: 20 mi. S of Nata, *D'Arcy & Croat 4120* (MO); Río Coclé, W of Penonomé, *Folsom 2920* (MO). HERRERA: alrededores de Océ, *Diaz 13A* (GH, MO). LOS SANTOS: Río Tonosí, vicinity of Tonosí, *Lewis et al. 1575* (MO). PANAMÁ: area around Madden Dam, 50–80 m, *Huft 1775* (MO); near Tapia River, Juan Diaz region, *Maxon & Harvey 6750* (GH); roadside between Chepo and Río Bayano, *Porter 5170* (MO); Macapale Island in Madden Lake, *Tyson 5501* (MO); weedy roadsides within 1 mi. of Chepo, *Wilbur & Luteyn 11799* (GH, MO).

Moritzia DC. in Meisner, *Pl. Vasc. Gen.* 1: 280; 2: 188. 1840. TYPE: *Moritzia ciliata* (Cham.) DC. in Meisner, *Pl. Vasc. Gen.* 2: 188. 1840.

Erect perennial herbs. Basal leaves often forming a spreading, open rosette, the cauline leaves alternate and usually considerably smaller than the basal ones. Inflorescence terminal, ebracteate, a sparsely branched cyme of spikes or racemes. Flowers bisexual; calyx tubular to narrowly campanulate; corolla tubular with spreading lobes, 5-merous, the lobes ovate to deltate, the tube with protuberances or tufts of hairs in the mouth; stamens 5, on short filaments, the anthers oblong; inserted above the middle of the corolla tube; ovary 4-lobed, the style gynobasic, the stigma obscurely bilobed. Nutlets solitary by abortion, erect, smooth to muricate but lacking spines.

Moritzia is an essentially South American genus of five species, only one of which, *M. lindenii*, extends into Central America. It is closely related to *Thaumatocaryon* (Johnston, 1924, 1927), from which it differs in having all of the leaves alternate and in lacking protuberances in the mouth of the corolla tube.

Moritzia lindenii (A. DC.) Gürke ex Benth. in Engl. & Prantl, *Nat. Pflanzenfam.* 4(3): 121. 1894. *Meratia lindenii* A. DC. in DC., *Prodr.* 10: 104. 1846. TYPE: Venezuela. Distrito Federal: Caracas, *Linden 944* (not seen).

Erect perennial herb to 50 cm tall, the stems strigose. Basal leaves sessile or on broad petioles to 5 cm long, narrowly elliptic to lanceolate or oblanceolate, 8–16 cm long, 1–3.5 cm wide, the apex acute, the base atten-

uate, the margin entire, the adaxial surface strigose, the abaxial surface strigose, the cauline leaves sessile, lanceolate to lance-ovate, 2.5–7 cm long, 0.4–1.4 cm wide, the apex attenuate to acuminate, the base acute, the margin entire, strigose on both surfaces. Inflorescences terminal, cymose, 3–10 cm long, the branches strigose. Flowers bisexual; calyx cylindrical, the 5 lobes lanceolate, 1.5–2.2 mm long, strigose; corolla blue, tubular with spreading lobes, 5-merous, the lobes widely ovate to depressed ovate, 0.9–1.3 mm long, the tube 2–2.4 mm long, pubescent in the mouth, strigillose outside; stamens 5, the anthers ellipsoid, 0.6–1 mm long, sessile, inserted just below the mouth of the corolla tube; ovary 4-lobed, the style gynobasic, 0.9–1.1 mm long, the stigma capitate. Nutlet ovoid, 2–2.5 mm long, muricate.

Distribution. *Moritzia lindenii* ranges from Venezuela, Colombia, and Ecuador north to Panama and adjacent Costa Rica. It occurs above 3,000 m in elevation. In Panama, it is known only from the province of Bocas del Toro but may be in upland Chiriquí as well.

Moritzia lindenii has been collected only once in Panama, although several collections are known from adjacent areas of Costa Rica. It is expected at high elevations in the same general region as *Cynoglossum* and *Hackelia*, the other two blue-flowered, herbaceous Boraginaceae known from Panama. It differs from members of these genera by lacking spines on its nutlets, only one of which develops to maturity, in contrast with the glochidiate spines on the four nutlets of *Cynoglossum* and *Hackelia*.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Cerro Fabrega and vicinity near Costa Rican frontier, south of summit, 3,150–3,335 m, *Weston 10162* (MO).

Tournefortia L., *Sp. Pl.* 140. 1753. TYPE: *Tournefortia hirsutissima* L., *Sp. Pl.* 140. 1753; I. M. Johnston, *Contr. Gray Herb.* 92: 66. 1930.

Small trees, shrubs, or woody vines. Leaves alternate or rarely opposite, petiolate or rarely

sessile, entire. Inflorescence terminal or internodal, dense to lax, a sparsely to profusely branched cyme. Flowers bisexual; sepals 5, one often exceeding the others in length, persistent; corolla white to green or yellow-green, tubular, with 5 spreading lobes; stamens 5, the anthers usually sessile or nearly so, borne within the corolla tube; ovary ovoid to globose, 4-locular, the style terminal or absent, the stigma conical. Fruit drupaceous, often white at maturity, later drying and separating into 2 or 4 bony nutlets containing 1 or 2 seeds.

Tournefortia includes about 150 species and has representatives in most warm areas of the world, although most species occur in

the Neotropics. *Mallatonia* (Griseb.) Britton, *Argusia* Amman, and *Messerschmidia* L. ex Hebenstreit have been treated as distinct by several authors, but Nowicke & Skvarla (1974) showed that pollen morphology does not support their continued separation. The three species that have been placed in these segregate genera differ from other members of *Tournefortia* in being strand plants with a pronounced corky exocarp and a similar sericeous indument.

Species of *Tournefortia* vary in habit. Most Panamanian species are lianas, sprawling shrubs, or sparsely branched erect shrubs, only a few becoming small trees. There often appears to be considerable variation in habit within a single species.

KEY TO THE SPECIES OF *TOURNEFORTIA* IN PANAMA

- 1a. Plants vining; fruits distinctly 4-lobed; the anthers apically connate (sect. *Cyphocyema* I. M. Johnston).
 - 2a. Leaves densely white puberulent to tomentose below; corolla tube 2–2.3 mm long *T. volubilis*
 - 2b. Leaves evenly short-strigillose below; corolla tube 3.3–5 mm long *T. maculata*
- 1b. Plants various in habit; fruit not deeply 4-lobed; the anthers free (sect. *Tournefortia*).
 - 3a. Leaves opposite.
 - 4a. Stems densely puberulent *T. ramonensis*
 - 4b. Stems densely and unevenly pubescent to hirsute *T. johnstonii*
 - 3b. Leaves alternate.
 - 5a. Corolla tube 10–13 mm long *T. angustiflora*
 - 5b. Corolla tube up to 10 mm long.
 - 6a. Stems shaggy-villose, the hairs 3–4 mm long; sepals 5.5–7.5 mm long *T. cuspidata*
 - 6b. Stems glabrous or with hairs less than 1.5 mm long; sepals less than 5 mm long.
 - 7a. Corolla lobes 3–4.5 mm long.
 - 8a. Corolla tube white with green stripes, 3.5–5 mm long; sepals 1.7–3.2 mm long; anthers bilobed, pendent in the mouth of the corolla tube *T. multiflora*
 - 8b. Corolla green to yellow-green, the tube 7–10 mm long; sepals 3.5–5 mm long; anthers lanceolate, sessile and inserted below the mouth of the corolla tube *T. urceolata*
 - 7b. Corolla lobes 1–3 mm long.
 - 9a. Sepals up to 2 mm long.
 - 10a. Corolla tube 5.5–6.5 mm long, the lobes 2.3–3 mm long; tertiary veins obscure *T. bicolor*
 - 10b. Corolla 3.5–4 mm long, the lobes 1.5–2 mm long; tertiary veins evident *T. glabra*
 - 9b. Sepals longer than 2 mm.
 - 11a. Corolla tube 9–9.5 mm long; tertiary veins obscure *T. tacarcunensis*
 - 11b. Corolla tube 3–6 mm long; tertiary veins evident.
 - 12a. Sepals 4.3–4.5 mm long *T. brenesii*
 - 12b. Sepals 2.5–4 mm long.
 - 13a. Stems strigose to hirsute; leaves strigose; corolla lobes 1–1.6 mm long *T. hirsutissima*
 - 13b. Stems glabrous or sparsely strigillose; leaves essentially glabrous; corolla lobes 2–2.5 mm long *T. longispica*

Tournefortia angustiflora Ruíz Lopez & Pavón, Fl. Peruv. 2: 25, pl. 151. 1799.
TYPE: Peru. Huánuco: Chicoplaya and Pueblo Nuevo, *Hipólito Ruíz & José Pavón s.n.* (not seen).

Scandent shrub to 1 m tall, occasionally a liana or tree to 5 m tall, the twigs glabrous to puberulent. Leaves alternate; petioles 5–12(–16) mm long, sparsely strigillose to puberulent; blade lance-ovate to lanceolate, 6–

15(-17) cm long, 2-6(-8) cm wide, the apex acuminate to attenuate, the base acute to cuneate, the margin entire, the adaxial surface sparsely strigillose to nearly glabrous, the abaxial surface with short, appressed hairs along the veins. Inflorescence terminal or internodal, a sparsely branched cyme, the peduncle (1-)2-4(-8) cm long, strigillose or puberulent to nearly glabrous, the fertile branches recurved, 2-9(-14) cm long. Flowers sessile, borne 2-4 mm apart; sepals 5, triangular, 1.2-1.6 mm long, sparsely strigillose; corolla white, 5-merous, the lobes ovate, 2-2.6 mm long, the tube 10-13 mm long, strigillose outside, puberulent on the inner surface of the lobes; stamens 5, the anthers lanceoloid, 2.5-3 mm long, sessile, inserted in the lower half of the corolla tube; ovary globose, ca. 1 mm long, the style to 0.8 mm long or lacking, the stigma conical. Fruits white, ovoid, often slightly inequilateral, 3-5 mm long, glabrous.

Distribution. *Tournefortia angustiflora* is wide-ranging and common in wet forests from Mexico south through northwestern South America to Peru, from sea level to 600 m in elevation. It is known from most provinces in Panama and is probably in all of them.

Tournefortia angustiflora is distinctive within the genus in having narrow, tubular corollas more than 1 cm long and somewhat asymmetrical fruits. It is vegetatively similar to *T. bicolor*, but the two are quite different when fertile.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Daytonia Farm, region of Almirante, *Cooper 166* (GH); 10-15 mi. inland from mouth of Changuinola River, *Lewis et al. 876* (GH, MO); Chiriquí Lagoon, Water Valley, *Wedel 1600, 1785* (GH, MO), *1802* (MO), *1832* (GH, MO); Chiriquí Lagoon, Old Bank Island, *Wedel 1880, 2004* (GH, MO); Chiriquí Lagoon, Isla Colón, *Wedel 2867, 2960* (GH, MO). CANAL AREA: W end of Gatún Lake Dam, *Blum & Tyson 2000* (MO); Barro Colorado Island, *Croat 7018, 8677, 9100* (MO); *Foster 1681* (GH); alluvial bottom near Bohio, 10-20 m, *Maxon 4777* (GH); between Gorgona and Mamei, 10-30 m, *Pittier 2259* (GH); valley of Masambi on the road to Las Cascadas Plantation, 20-100 m, *Pittier 2592* (GH); Fort San Lorenzo, *Porter et al. 5009* (MO); Barro Colorado Island, *Shattuck 495* (MO); *Woodworth & Vestal 378*

(A, MO). COCLÉ: El Valle de Antón, 600 m, *Allen 2059* (GH, MO); summit of Cerro Pilón, above El Valle de Antón, 2,700 ft., *Dwyer et al. 4501* (MO); 46 km N from Penonomé on road to Coclesito, 100 ft., *Hammel 1695* (MO); hills NE of El Valle de Antón, 2,000 ft., *Lewis et al. 1799* (MO); Boca del Toabre at confluence of Río Toabre and Río Coclé del Norte, *Lewis et al. 5508* (MO). COLÓN: near Nuevo Tonosí 2 mi. from Portobelo on road to Nombre de Dios, 100 m, *Croat 33523* (MO); along Río Guanche about 1-2 km from Portobelo Highway toward Cerro Bruja, 0-50 m, *Huft & Knapp 1783* (MO); along dirt trail, 4 km NW of Salamanca, 13 km NE of Buenos Aires, 340-410 m, *Nee 9063* (MO). DARIÉN: Río Tuqueza below Quebrada Venado, *Bristan 1076* (GH); El Real, Quebrada Trapiche, *Duke & Bristan 315* (MO); vicinity of Santa Fe, *Duke 9496* (MO); Cocalito, *Dwyer 4465* (MO (2)). HERRERA: roadside between El Potrero and Las Minas, *Croat 9655* (MO); 12 mi. S of Ocu on Las Minas road, *Graham 235* (GH); Punta Mala, *Tyson 2714* (MO); 10 mi. S of Ocu, *Tyson et al. 2863* (MO). PANAMÁ: Panamerican Highway 22 km E of Bayano Bridge, near bridge over stream, less than 200 m, *Folsom 1396* (MO); Sabanas near Chepo, *Hunter & Allen 94* (MO); Alahajuela Chagres Valley, 30-100 m, *Pittier 2371* (GH). SAN BLAS: mainland opposite Ailigandi, from mouth of Ailigandi River to 2.5 mi. inland, *Lewis et al. 167* (MO).

***Tournefortia bicolor* Sw., Prodr. 40. 1788. TYPE: Jamaica (not seen).**

Tournefortia laevigata Lam., *Encycl.* 1: 416. 1791. TYPE: Guadeloupe, *Badier s.n.* (not seen).

Tournefortia nitida Kunth in Humb., *Bonpl. & Kunth, Nov. Gen. Sp.* 3: 84. 1819. TYPE: Colombia. Bolívar: near Cartagena (not seen).

Tournefortia bicolor Sw. var. *calycosa* J. D. Smith, *Bot. Gaz. (Crawfordsville)* 14: 27. 1889. TYPE: Guatemala. Alta Verapaz: Pansamalá, 3,800 ft., *H. von Tuerckheim 980* (holotype, US 944708).

Woody vine, shrub, or small tree to 3(-7) m tall, the twigs glabrous or sparsely short-strigillose. Leaves alternate; petioles (0.8-)1-2 cm long, glabrous or very sparsely short-strigillose; leaf blade elliptic or ovate to narrowly elliptic or lance-ovate, (8-)11-14(-19) cm long, (3.5-)5-8 cm wide, the apex acuminate to acute, the base obtuse to rounded or less commonly acute, the margin entire, the adaxial and abaxial surfaces glabrous or with a few widely scattered, appressed hairs, the tertiary veins obscure. Inflorescence terminal, a dense cyme, the peduncle to 3 mm long, the branches glabrous to sparsely strigillose, the fertile branches 2-5 cm long. Flowers sessile, crowded, usually borne less than 2 mm apart; sepals 5, lanceolate, 1.5-2 mm long, sparsely to evenly strigillose; corolla

white, sometimes with a greenish tint, 5-merous, the lobes ovate and often apiculate, 2.3–3 mm long, the tube 5.5–6.5 mm long, strigillose outside; stamens 5, the anthers lanceoloid, 1.3–2 mm long, sessile, inserted below the middle of the corolla tube; ovary globose, 0.4–0.6 mm long, the stigma sessile, conical. Fruits ovoid, white, 3–5 mm long, glabrous.

Distribution. *Tournefortia bicolor* is common in wet forest from sea level to 1,800 m throughout the Neotropics, ranging from Mexico through Central America and the West Indies to northern and western South America. In Panama, it is known from all provinces except Herrera.

Tournefortia bicolor is closely related to *T. hirsutissima* (Johnston, 1935) but has generally been considered to be distinct (Nowicke, 1969; Gibson, 1970). Nash & Moreno (1981), however, treated *T. bicolor* as a form of *T. hirsutissima*. Both species are widespread in the Neotropics, and although *T. bicolor* generally occurs in wetter habitats, the two can be found together at numerous localities such as along the shore of Barro Colorado Island (Croat, 1978). *Tournefortia bicolor* differs from *T. hirsutissima* in being essentially glabrous and in having sepals 1.5–2 mm long, a corolla 5.5–6.4 mm long, and corolla lobes 2.3–3 mm long; *T. hirsutissima* is generally pubescent, the sepals are 2.5–4 mm long, and the corollas are 3.5–5.3 mm long with lobes 1–1.6 mm long. Morphological and ecological data strongly support recognition of *T. bicolor*.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Río San Pedro, *Gordon 78C* (MO); along runway at Bocas, *Lazor et al. 2347* (MO); Chiriquí Lagoon, Water Valley, *Wedel 986, 1838* (GH, MO); Chiriquí Lagoon, Old Bank Island, *Wedel 1952, 1992, 2090* (GH, MO); Chiriquí Lagoon, Fish Creek Hills, *Wedel 2427* (GH, MO); Chiriquí Lagoon, Cocoa Cay, *Wedel 2877* (GH, MO). CANAL AREA: Victoria Fill, near Miraflores Locks, *Allen 1713* (GH, MO); east slope of Cerro Jefe, 2,700 ft., *Blum & Duke 2190* (MO); Barro Colorado Island, *Croat 7686, 7822, 8373* (MO); hills S of Pedro Locks, *Croat 9176* (MO); Barro Colorado Island, *Croat 9560* (MO); road from Gatún Locks to old French Canal and vicinity, *Duke & Mussell 6654* (GH, MO); near

Gatún Station, Panama railroad, *Hayes s.n.* (GH); Chagres, *Fendler 232* (MO); 1 mi. from Gaillard Highway on small dirt track off Chiva Chiva, 0–25 m, *Knapp & Schmalzel 4850* (MO); 2 mi. W of Canal Zone–Ferry Thatcher bridge, *Lazor 2189* (MO); Bella Vista, *Piper 5380* (GH); Barro Colorado Island, *Shattuck 807* (MO (2)), *1064, s.n.* (MO); Fort Clayton near old hospital building #519, *Tyson & Blum 3932* (MO); near Gorgas Memorial Lab, *White 83* (GH, MO); Barro Colorado Island, *Woodworth & Vestal 345* (GH, MO), *482* (GH), *514, 615* (GH, MO). CHIRIQUÍ: disturbed cloud forest at Monte Rey about Boquete, *Croat 15770* (GH, MO); windswept ridge 8 km N of Los Planes de Hornito, I.R.H.E. Fortuna Hydroelectric Project, *Knapp 4982* (MO); Quebrada Melliza, 6 mi. S of Puerto Armuelles, 0–150 m, *Liesner 507* (GH, MO). COCLÉ: El Valle, *Aguilar 47* (MO); N rim of El Valle de Antón, 600–1,000 m, *Allen 1738* (GH, MO); roadside S of El Valle, *D'Arcy et al. 13321* (MO); forest behind Club Campestre, *Duke 13259* (MO (2)); hills NE of El Valle de Antón, 2,000 ft., *Lewis et al. 1707* (GH, MO); David, 1,000–1,300 m, *Pittier 2839* (GH); 4 mi. past Llano Grande on road to Cascajal, 200 yards past continental divide, 450–500 m, *Sytsma 3929* (MO); 4 mi. past Llano Grande on road to Cascajal, rocky faced hill ca. 2 km W along continental divide, 600 m, *Sytsma 3961* (MO); 4 mi. past Llano Grande on road to Cascajal, rocky faced hill ca. 2 km W along continental divide, 600 m, *Sytsma 3980* (MO). COLÓN: Portobelo, *Billberg 270* (GH); Santa Rita Ridge lumber road, *Correa & Dressler 737* (MO); Santa Rita, camino a la zona maderera a 15 km NE de la Transisthmica, *Correa & Dressler 1137* (MO); Miguel de la Borda, *Croat 9853* (MO); Santa Rita Ridge, *Croat 13864* (MO); vicinity of Río Indio on road from Portobelo to Nombre de Dios, *Croat 33585* (MO); along Río Iganita near bridge along Portobelo road, less than 50 m, *Croat 49777* (MO); Santa Rita lumber road, near Agua Clara weather station, *Dressler 3851* (MO); Santa Rita East Ridge, *Dwyer & Correa 8401* (MO (2)); along Río Guancho, 1–4 km S of the Portobelo highway, 0–50 m, *Knapp et al. 4610* (MO); Santa Rita Ridge, ca. 4–5.5 mi. E of Transisthmian Highway, *Lewis et al. 5252* (MO); Santa Rita Ridge, ca. 4–5.5 mi. E of Transisthmian Highway, *Lewis et al. 5285* (GH, MO); 10 mi. SW of Portobelo, 2–4 mi. from coast, 10–200 m, *Liesner 1079* (GH, MO); thickets and weedy roadside along Portobelo road at bridge over Río Viejo, 9 m, *Nee & Tyson 10896* (MO (2)). DARIÉN: Punta Guayabo Grande, 0–50 m, *Antonio & Hahn 4225* (MO); Cerca de El Real al lado de quebrada, *Correa & Lazor 1527* (MO); a lo largo de la unión del Río Tuira con El Chucanaque, a lo largo del ultimo hasta Río Tupisa, *Correa & Lazor 1543* (MO); Río Sambu, 0–5 mi. above Río Venado, *Duke 9270* (MO); Isla Casaya, *Duke 10379* (MO); Isla Pedro Gonzalez, *Duke 10405* (MO); Río Pinas, *Duke 10558* (MO); coastal thicket near Jaqué, *Duke 10665* (MO); Hydro Camp Pico Pendejo in Monsoon forest on Río Sabana, 50 ft., *Duke 15450* (MO); Mannene to the mouth of the Río Cuasi, *Kirkbride & Bristan 1500* (MO); trail between Caña and Boca de Cupe, vicinity of El Real, along road to Pirre River, *Stern et al. 619* (GH, MO); vicinity of Caña, 1,750 ft., *Stern et al. 692* (GH, MO); Tucute, *Terry & Terry 1397* (GH, MO). LOS SANTOS: Punta Mala, *Croat 9759* (MO); *D'Arcy & Croat 4218* (MO); Loma Prieta, 800–900 m, *Duke 11848* (MO); road between Tonosí and Guanica, *Stern et al. 33684*

(MO); Guayabo, several miles W of Tonosí, *Stern* 33704 (MO). PANAMÁ: Santa Lucía, Río San Pablo, near Pueblo Nuevo, *Barclay* 1799 (MO); San José Island, Canyon road, *Campbell* 3 (GH); along dirt road to Cerro Campana, *Correa & Dressler* 853 (A, MO); along road to Cerro Campana, *Croat* 14676 (MO); El Llano-Carti Road 8.2 mi. N of Interamerican Highway, 300–350 m, *Croat* 33701 (MO); middle slopes of Cerro Campana, ca. 1 mi. from Interamerican Highway, 150 m, *Croat* 35946 (MO); Cerro Campana, 800 m, *D'Arcy* 11143 (MO); alrededores de Chagres, *Diaz* 37 (MO); Cerro Jefe, *Duke* 9391, 9430 (MO); Río Pacora, just below confluence with Río Corso, *Duke* 12029 (MO); San José Island, along road between Bodega Bay and Río Mata Puerco, *Duke* 12056 (MO (2)); Tocumen, *Dwyer* 7238 (MO); Cerro Jefe, 2,900 ft., *Dwyer et al.* 7254 (GH, MO); San José Island, *Erlanson* 3, 87, 140 (GH); Chagres, *Fendler* 232 (GH); Taboga Island, behind rocky beach, near hotel, sea level, *Gentry* 5745 (MO); Llano-Carti Road, 200 m, *Hahn* 345 (MO); forest and roadside between 6–12 km north of El Llano on Carti road, 1,200 ft., *Hammel* 854 (MO); 10 mi. from Pan-American Highway on the road from El Llano to Carti, 350 m, *Huft et al.* 1875 (MO); San José Island, *Johnston* 629, 758, 1355 (GH); 12–16 km above Pan-Am Highway on road from El Llano to Carti-Tupile, 150–400 m, *Kennedy et al.* 3109 (GH, MO); along road up to Cerro Campana, along edge of montane forest, *Lazor* 2219 (MO); Panama City, *Macbride* 2730 (MO); El Llano-Carti Road, 8.5 km from highway, 1,200 ft., *Mori* 4556 (MO); El Llano-Carti Road, 8.5 km from Inter-American Highway, 350 m, *Mori et al.* 4556 (MO); El Llano-Carti Road, 8.5 km from Inter-American Highway, 350 m, *Mori & Kallunki* 5173 (MO); 6.5 km by road N of Lago Cerro Azul, 650–730 m, *Nee* 9311 (MO); Cerro Jefe, 4.7 mi. above Goofy Lake, 800 m, *Sytsma et al.* 2812 (MO); El Llano-Carti Road, 9 km above Pan-American Highway, 900–1,000 ft., *Sytsma* 3096 (MO); 6 km S of El Valle on highway 71, 2,400 ft., *Sytsma & D'Arcy* 3558 (MO); El Llano-Carti Road, 6 mi. from Pan-American Highway, 300–400 m, *Sytsma* 4001 (MO); Isla Taboga, 0–186 m, *Woodson et al.* 1538 (MO). SAN BLAS: Permé, *Cooper* 218 (GH); Río Ailigandi, *Duke* 10834 (MO); mainland opposite Ailigandi, from mouth of Ailigandi river to 2.5 mi. inland, *Lewis et al.* 65 (MO); near Puerto Obaldía, W of village, on foot-trail to La Bonga, 50–140 m, *McPherson* 6963 (MO). VERAGUAS: along last major stream between Santa Fe and Escuela Agrícola Alto Piedras, 420 m, *Croat & Folsom* 33832 (MO); Río Santa María near bridge below Santa Fe, 300–400 m, *Knapp & Kress* 4326 (MO); 2 mi. W of Santa Fe, 400–800 m, *Liesner* 838 (GH, MO (2)).

Tournefortia brenesii Standley, *Publ. Field Mus. Nat. Hist., Bot. Ser.* 18: 989. 1938.
TYPE: Costa Rica. Alajuela: El Silencio (Los Angeles) de San Ramón, Feb. 1933, *Brenes* 17103 (holotype, F 859855).

Shrub to 3 m tall, the branches brown-strigose to pubescent, later glabrous. Leaves alternate but often densely clustered near the ends of branches; petioles 3–10(–27) mm

long, glabrous to brown pubescent; leaf blades lanceolate, 9.5–17(–19) cm long, (2–)2.5–5.5(–6.3) cm wide, the apex acuminate to attenuate, the base acute, the margin entire to unevenly undulate or dentate, the adaxial surface glabrous, the abaxial surface glabrous except for scattered short appressed hairs along the secondary veins, the tertiary and quarternary veins clearly visible. Inflorescence terminal or subterminal, cymose, branching dichotomously 2–4 times, the peduncle to 11 cm long, brown puberulent to strigillose. Flowers on short pedicels to 5 mm long, borne (2–)4–10 mm apart; sepals 5, ovate to lanceolate, 4.3–4.5 mm long, ca. 1.7 mm wide, glabrous to sparsely strigillose; corolla white, tubular with spreading ovate to lanceolate lobes, these acute at the apex, 2.6–2.7 mm long, the tube 4.8–5 mm long, strigillose outside; stamens 5, the anthers oblong to lanceoloid, sessile or nearly so, inserted in the middle of the corolla tube; ovary globose, ca. 1 mm long, the disc crateriform, the style ca. 1 mm long, the stigma pyramidal. Fruit ovoid, 6–8 mm long, 5–6 mm wide, white at maturity, often capped by the persistent stigma.

Distribution. *Tournefortia brenesii* is restricted to cloud forests from 800–1,350 m in elevation in Panama and Costa Rica. In Panama it is known only from the province of Veraguas.

Tournefortia brenesii is distinct in its compact habit of growth, with the leaves clustered densely near the branch tips, and broad, accrescent sepals.

Additional specimens examined. PANAMA. VERAGUAS: vicinity of Escuela Agricultura Alto Piedra near Santa Fe, along trail to top of Cerro Tute, 3,500 ft., *Antonio* 4957 (MO); Cerro Tute, ridge up from former Escuela Agrícola, Santa Fe, 1,000–1,300 m, *Hamilton & Dressler* 3080 (MO); ridge of Cordillera de Tute, trail to Cerro Tute, above Escuela Agrícola Alto de Piedra, just W of Santa Fe, 800–1,350 m, *Knapp & Dressler* 5403 (MO); Cerro Tute, ca. 10 mi. NW of Santa Fe, on ridgetop in cloud forest, above 1,000 m, *Mori* 6760 (MO).

Tournefortia cuspidata Kunth in Humb., *Bonpl. & Kunth, Nov. Gen. Sp.* 3: 83.

1818. TYPE: Ecuador. Guayas: Guayaquil, *Humboldt & Bonpland s.n.* (holotype, P, not seen).

Tournefortia obscura A. DC. in DC., Prodr. 9: 517. 1845. TYPE: Guyana: *Schomburgk 571* (holotype, G-DC, not seen; microfiche, MO).

Scandent woody vine or sprawling shrub to 2 m tall, the twigs villose with hairs to 4 mm long. Leaves alternate; petioles 3–8 mm long, stout, shaggy-villose; blade lance-ovate, elliptic, ovate, or rarely obovate, 8–13(–19) cm long, 3–6(–9) cm wide, the apex acuminate, the base acute to obtuse, the margin entire, the adaxial surface strigose, the abaxial surface strigose to nearly villous, especially along the veins. Inflorescence terminal, a few- to much-branched, dense cyme, the sterile portions of branches shaggy villous. Flowers sessile, very closely spaced; sepals lanceolate, 5.5–7.5 mm long, strigose to hirsute; corolla white to green, 5-merous, the lobes ovate, 1–1.8 mm long, the tube 6.5–8 mm long, strigose to sericeous on the outside; stamens 5, the anthers lanceoloid, 1.3–1.5 mm long, sessile, inserted beneath the middle of the corolla tube; ovary globose to ovoid, ca. 1 mm long, the style 0.4–0.5 mm long, the stigma conical. Fruits ovoid, 3–4.5 mm long, white at maturity, breaking into (2–)4 nutlets at maturity, glabrous.

Distribution. *Tournefortia cuspidata* is common in disturbed areas of moist to wet forests at elevations below 400 m from Mexico to South America, and it occurs on Trinidad and Tobago. In Panama it is known from Bocas del Toro, Canal Area, Coclé, Colón, Darién, Panamá, and San Blas.

Tournefortia cuspidata is a distinctive species readily recognized by its shaggy, villose twigs with the hairs up to 4 mm long and sepals greater than 5 mm long. This is one of the most commonly collected species in southern Central America and northern South America. It is perhaps most closely related to *T. hirsutissima* but differs in its much longer hairs and sepals. Although the long hairs on the stems are usually diagnostic,

these are greatly reduced in plants from adjacent Chocó, Colombia.

Additional specimens examined. PANAMA. BOCAS DEL TORO: along railroad tracks near station at Milla 5, *Croat & Porter 16493* (MO); Changuinola to 5 mi. S at junction of ríos Changuinola and Terebe, 100–200 ft., *Lewis et al. 951* (GH, MO); Almirante, near Dos Milla, *McDaniel 5138* (MO); Chiriquí Lagoon, Water Valley, *Wedel 770* (GH, MO), *1282* (MO), *1674* (GH, MO); Chiriquí Lagoon, Old Bank Island, *Wedel 1959* (GH, MO); Chiriquí Lagoon, Little Bocas, *Wedel 2510* (MO), *2559* (GH, MO); Chiriquí Lagoon, Isla Colón, *Wedel 2961* (GH). CANAL AREA: France Field, *Blum & Dwyer 2125a* (MO); Gamboa Navy Pipe Line along main dirt road, *Correa & Haines 544* (MO); Barro Colorado Island, *Croat 4207*, *4683*, *7194*, *7415*, *7684*, *7748* (MO); road S-10, N of Escobal, *Croat 12445*, *13114* (MO); Gaillard Highway between Paraiso and the Continental Divide, *Croat 14833* (MO); Pipeline Road to 18 km N of Gamboa, *D'Arcy s.n.* (MO); Barro Colorado Island, *Dwyer et al. 8447* (MO); Gamboa, Naval Reservation, *Ebinger 892* (GH, MO); Pipeline Road, 5–6 mi. N of Gamboa, 100–200 m, *Gentry 6671* (MO); Barro Colorado Island, *Hayden 41* (MO); NW shore of Gatún Lake, ca. 4 mi. S of Río Chagres, *Lewis 1823* (MO); Pipeline Road between mile markers 0 and 11.1, ca. 16 mi. N of Gamboa, *Lewis et al. 5452* (MO); on Pipeline Road, 14.4 km from Chagres Airport Road, 0–100 m, *Mori & Kallunki 2062* (MO); Barro Colorado Island, *Shattuck 100* (GH, MO (2)), *676* (GH, MO (3)), *957* (MO); *Starry 228* (MO); *Whetmore & Abbe 201* (GH (2), MO); *Whetmore & Woodworth 854* (GH); along the margin of Pipeline Road N of Gamboa, *Wilbur & Weaver 11267* (MO); Barro Colorado Island, *Woodworth & Vestal 328* (GH, MO), *523* (GH). COCLÉ: forest on hills above road 18 km past Sardinilla on way to Nombre de Dios, 150–300 m, *Croat 26105* (MO); around Rivera Sawmill, 7 km N of El Copé, 700–850 m, *Folsom et al. 5696* (MO); along Río San Juan below its junction with Río Tife, 1,200 ft., *Hammel 3390* (MO). COLÓN: forested area near Guasimo along river, *Croat 9968* (MO); Peluca, ca. 2.7 km from Transisthmian Highway on road to Nombre de Dios, *Kennedy 2638* (MO); along Río Boquerón above Mina Boquerón #1 (manganese mine), main valley of the Río Boquerón, 100–200 m, *Knapp & Sytsma 2465* (MO); along Río Boquerón near No.1 (manganese mine), E of Salamanca, 50 m, *Knapp et al. 5821A* (MO); roadside and woods near bridge over Quebrada La Furnia on highway 5-8 (82), road to Pinas, 10 m, *Mori & Kallunki 1946* (GH, MO). DARIÉN: headwaters of Río Chico, 500–750 ft., *Allen 4638* (MO); 110 mi. from Bayano Dam Bridge, vicinity of Canglon, trail to south, 1 km W of bridge in Canglon, 50 ft., *Antonio 4584* (MO); camino de El Real a Pinogana, *Correa & Lazor 1555* (MO); vicinity of El Real along road to airport, *Croat & Porter 15445* (MO); El Real, *D'Arcy 5512* (MO); 2–3 mi. SE of El Real, *Duke 4853* (MO); road from El Real to Pinogana, *Duke 5001* (GH (2), MO); Isla Boca Grande, *Duke 8843* (MO); Río Sambu, 0–5 mi. above Río Venado, *Duke 9268* (MO); Enseñada del Guayabo, 16–19 km SE of Jaqué, *Garwood 921* (MO); Manene to mouth of Río Cuasi, *Kirkbride & Bristan 1415* (MO); Río Tuquesa, at lower Tuquesa Mining Company camp called Charco Chiva, 100 m, *Mori*

6995 (MO); vicinity of Yaviza, along Río Chucunaque, El Punteadero bridge, Inter-American Highway over Río Chucunaque, a short distance down river from Yaviza, *Stern et al.* 170 (GH, MO); vicinity of Paya, Río Paya, trail between Paya and Payita, *Stern et al.* 363 (GH, MO); Gold Mine at Caña, 480 m, *Sullivan* 749 (MO); 3 mi. E of Santa Fe, *Tyson et al.* 4652 (MO); 2 mi. E of Santa Fe, *Tyson* 4818 (MO). PANAMÁ: Río Pita, 0–2 mi. above tidal limit, *Duke* 4793 (MO (2)); forests along headwaters of Río Corso, off Río Pacora, 500 m, *Duke* 11929 (MO); N of El Llano, 500–800 m, *Gentry* 5560 (MO); Pipeline Road, 50 m, *Hamilton et al.* 3266 (MO); 10 mi. from Pan-American Highway on the road from El Llano to Carti, 350 m, *Huft et al.* 1874 (MO); Alcalde Diaz, *Jaen* 23 (MO); forest edges along Río Pirati, about ½ hour walk from Pan-American Highway, foothills of the Serranía de Maje, 50–100 m, *Knapp & Mallet* 5164 (MO); El Llano–Carti Road, 6–10 mi. from Pan-American Highway, 400 m, *Miller et al.* 857 (MO); along the Pan-American Highway 6.5 mi. E of highway checkpoint at turnoff to Chepo, *Miller et al.* 1019 (MO); Gorgas Memorial Labs yellow fever research camp, ca. 25 km NE of Cerro Azul on Río Piedras, 550 m, *Mori & Kallunki* 3464 (MO); Arenoso, lower Río Trinidad, 26–50 m, *Seibert* 625 (GH (2), MO); 2 mi. E of El Llano, *Tyson* 1737 (MO); 5 mi. E of Canita or 23 mi. E of Chepo, *Tyson & Smith* 4152 (MO); 1 mi. E of El Llano, *Tyson* 6883 (MO); La Rana de Oro, Pedregal, *Villamil* 33 (MO); wet savanna E of Pacora, 25 m, *Woodson et al.* 721 (MO), 722 (GH (2), MO). SAN BLAS: El Llano–Carti Road, 350 m, *de Nevers & Herrera* 4222 (MO); trail from Puerto Obaldía to La Bonga, tributary of the Río Armila, ca. 2 hours walk from Puerto Obaldía, 0–50 m, *Knapp & Mallet* 4679 (MO); along newly cut road from El Llano to Carti-Tupile, continental divide to 1 mi. from divide, 300–500 m, *Liesner* 1297 (GH, MO).

***Tournefortia glabra* L., Sp. Pl. 141. 1753.**

TYPE: without locality or collector (holotype, LINN (Savage Catalog number 193.5), not seen; microfiche, MO).

Small tree or shrub to 5(–10) m tall, the twigs glabrous to sparsely strigillose. Leaves alternate; petioles 1–4(–5) cm long, sparsely strigillose to nearly glabrous; leaf blade narrowly elliptic to lance-obovate, (8–)12–18 (–25) cm long, (2.5–)5–8(–12) cm wide, the apex acuminate, the base attenuate and usually strongly decurrent, the margin entire, the adaxial surface sparsely strigillose to nearly glabrous, the abaxial surface with a few hairs scattered along the veins, the tertiary veins evident. Inflorescence internodal or terminal, a loosely branched cyme, the peduncle 3–8 (–14) cm long, sparsely strigillose to nearly glabrous, the branches 3–8(–10) cm long. Flowers sessile, borne (1–)2–3(–4) mm apart;

sepals lanceolate, 1–1.2 mm long, sparsely strigillose; corolla white or greenish white, 5-merous, the lobes lanceolate, 1.5–2 mm long, the tube 3.5–4 mm long, strigillose outside; stamens 5, the anthers ellipsoid, 0.6–1 mm long, sessile or nearly so, inserted above the middle of the corolla tube; ovary ovoid, 0.7–1.5 mm long, the disc crateriform to scarcely evident, the style 1–1.2 mm long, the stigma capitate. Fruits white at maturity, very broadly ovoid, 3–4 mm long, glabrous.

Distribution. *Tournefortia glabra* occurs in diverse moist to wet habitats from sea level to 2,700 m in elevation. It is found from Mexico through Central and South America and in the West Indies. In Panama, it is known from Bocas del Toro, Chiriquí, Coclé, Colón, Panamá, San Blas, and Veraguas.

Tournefortia glabra is one of the few small understory trees in the genus found in Central America. This species is vegetatively quite similar to *T. acutiflora* Martens & Galeotti of northern Central America and southern Mexico, but differs in having calyx lobes shorter than 1.5 mm long.

Additional specimens examined. PANAMA. BOCAS DEL TORO: region of Almirante, Daytonia farm, *Cooper* 376 (GH, MO); along road to Chiriquí Grande, 450 m, *McPherson* 7391 (MO); Chiriquí Lagoon, Water Valley, *Wedel* 1573, 1746 (GH, MO). CHIRIQUÍ: 12 mi. from Gualaca on road to Cerro Hornito, 1,300 m, *Antonio* 1751 (MO); Cerro Colorado Mine, 2 mi. from Lower Elevation Camp, 4,200 ft., *Antonio* 4906 (MO); Palo Alto–Boquete, 1,300–1,772 m, *Beliz* 215 (MO); 5.4 km del Hato del Volcán en el camino a Las Lagunas, *Correa & Lazor* 1461 (MO); E of Boquete along forested slopes and pastures on Cerro Azul near Quebrada Jaramillo, 1,500–1,620 m, *Croat* 26781 (GH, MO); Chiquero, Boquete, *Davidson* 552 (GH, MO); TTC-BMI Cloud Forest Litter Study Cerro Horqueta, 1,500 m, *Duke et al.* 13637 (MO); NW of Boquete, Cerro Horqueta, 5,000–5,800 ft., *Dwyer et al.* 478 (MO); Boquete, Finca Collins, 5,000 ft., *Dwyer & Hayden* 7644 (MO); Boquete, Fred Collins Finca, *Ebinger* 667 (MO); road to Río Serano, *Folsom et al.* 2107 (MO); path from Linares farm ca. 1,400 m to top of Cerro Hornito at 1,750 m, *Folsom et al.* 7227 (MO); Las Lagunas area W of Hato del Volcán, 1,400 m, *Hamilton & Stockwell* 3574 (MO); along Río Colorado, 1,200–1,400 m, *Hamilton & Krager* 3806 (MO); road along Río Palo Alto ca. 3 km NE of Boquete to the end, *Huft* 1858 (MO); Collins Finca, 2,000 m, *Kirkbride* 119 (MO); N of San Felix, 36.2 km by road from the Interamerican Highway, *Mori & Kallunki* 6017 (MO); Dos Lagunas, 4 km W of El Hato del Volcán, 1,300 m,

Mori & Bolten 7400 (MO); Las Lagunas, 2 mi. SW of El Volcán, 4,200 ft., *Tyson 850* (MO); Río Chiriquí Viejo valley, near Bambita, *White 46* (GH, MO); Finca Lerida to Peña Blanca, 1,750–2,000 m, *Woodson & Schery 285* (GH (2), MO); vicinity of Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al. 986* (GH, MO). COCLÉ: El Valle, 600–1,000 m, *Allen 1200* (GH), *1794* (GH, MO); La Mesa above El Valle, 810 m, *Croat 25298* (GH, MO); Cerro Pilon near El Valle, *Duke 12060* (MO); El Valle de Antón at the foot of Cerro Pilón, 2,000 ft., *Dwyer & Correa 7964* (MO); El Valle de Antón at the foot of Cerro Pilón, 2,000 ft., *Dwyer & Correa 7965* (MO); Cerro Pilón, 2,700 ft., *Dwyer & Lallathin 8610* (MO); vicinity of La Mesa above El Valle, 900 m, *Gentry 7408* (GH, MO); hills above El Valle, 1,000 m, *Gentry 6895* (MO); La Mesa region N of Cerro Gaital vicinity of El Valle, 2,400 ft., *Hammel 3899* (MO); El Valle de Antón, La Mesa, 1,000 m, *Kennedy et al. 3034* (MO); El Valle Wepcor site, on trail from end of road to the site, *Kirkbride 1088* (MO); foothills and summit of Cerro Caracoral, near La Mesa N of El Valle de Antón, 800–1,100 m, *Knapp 1111* (MO); Cerro Pilón, 900–1,173 m, *Liesner 768* (MO); along road above El Valle toward upper ridges above town, *Miller et al. 775* (MO); foot of Cerro Pilón, above El Valle de Antón, 2,000 ft., *Porter et al. 4640* (MO); NE slopes and summit of Cerro Caracoral, north rim of El Valle, 2,700–3,200 ft., *Sytsma 4051* (MO); trail to La Mesa about 4.5 mi. beyond El Valle de Antón, *Wilbur & Luteyn 11683* (MO). COLÓN: ridge top leading N from Río Escandaloso towards Cerro Bruja, 600 ft., *Hammel 2708* (MO). DARIÉN: between Quebrada Venado and Peje swamp on the headwaters of Río Tuquesa, *Bristan 1006* (MO); Río Ucurganti, *Bristan 1139* (MO); trail SE of Manene to Río Cuasi, *Hartman 12197* (MO); premontane rainforest 0–2 mi. E of Tres Bocas along the shortest headwater of Río Cuasi, *Kirkbride & Duke 1144* (MO (2)); Río Tuquesa, at middle Tuquesa Mining Company camp called Charco Peje, 250 m, *Mori 7002, 7093* (MO); Paya, Río Paya, *Stern et al. 396* (GH, MO). PANAMÁ: Cerro Campana, 600 m, *Antonio 1730* (MO); trail up to Campana Ridge, *Correa & Dresler 377* (MO (2)); forest near dam site south of Canita, *Croat 14531* (MO); cloud forest on Cerro Campana near FSU building, *Croat 14809* (MO); Cerro Campana, 800 m, *D'Arcy 11141* (MO); Cerro Campana, 2,500 ft., *D'Arcy & Hamilton 14931* (MO); Río Bayano, near crossing of Pan-Am Highway, above confluence with Río Chepo, *Duke 3974* (MO (2)), *3998* (MO); Piria-Canasas Trail near Piria, 100 m, *Duke 14330* (MO); area around Torti Arriba, *Folsom 5129* (MO); near top of Cerro Campana, above FSU cabin, *Gentry 5770* (MO); 3.8 mi. E of Río Ipeti, S along river and into lower slopes of Serranía de Maje, 50–200 m, *Huft & Jacobs 2002* (MO); near Cerro Campana, on trail radiating from end of road which passes Campana water tank, *Kirkbride & Hayden 312* (MO); forest edges along Río Pirati, about ½ hour walk from Pan-American Highway, foothills of the Serranía de Maje, 50–100 m, *Knapp & Mallet 5167* (MO); Cerro Campana, trails just inside entrance to Parque Nacional, 850 m, *Miller & Miller 995* (MO); Parque Nacional Cerro Campana, 2 km N of highway 707, 850 m, *Stein & Hamilton 1140* (MO); base of Serranía de Canasas, ca. 15 km SW of Canaza near Río Torti, 150 m, *Stein 1387* (MO); steep slopes S of Canita, 200 m, *Webster et al. 16885* (MO); lower slopes and trail to Cerro Cam-

pana, *Witherspoon 8400* (MO). SAN BLAS: El Llano-Carti Road, km 16.7, trail W to Río Carti Grande, 250–350 m, *de Nevers & Herrera 4177* (MO); along the headwaters of Río Mulatupo, *Elias 1751* (MO). VERAGUAS: El Cuchillo, near Cerro Tute, up from Santa Fe, 1,300 m, *Hamilton et al. 1240* (MO).

***Tournefortia hirsutissima* L., Sp. Pl. 140.**

1753. *Messerschmidia hirsutissima* (L.) Roemer & Schultes, Syst. Veg. 4: 451. 1819. TYPE: without locality or collector (holotype, LINN (Savage Catalog number 193.1), not seen; microfiche, MO).

Tournefortia schomburgkii DC., Prodr. 9: 517. 1845. TYPE: Guyana: 1837, *Schomburgk 70* (holotype, G-DC, not seen; microfiche, MO; isotype, K).

Woody vine, sprawling shrub, or small tree, the twigs strigose to hirsute. Leaves alternate; petioles (3–)8–15(–20) mm long, strigose to hirsute; leaf blade lance-ovate to narrowly elliptic, (7–)11–18(–20) cm long, (2.5–)3.5–6(–8) cm wide, the apex acuminate to acute, the base acute to obtuse, the margin entire, the adaxial surface strigose, the abaxial surface strigose to pubescent, the tertiary veins evident. Inflorescence terminal or rarely internodal or axillary, a much-branched, dense cyme, the peduncle (1–)2–4(–5) cm long, strigose to hirsute, the fertile branches 1.5–4(–6) cm long. Flowers sessile, borne 1–2(–3) mm apart; sepals lanceolate, 2.5–4 mm long, strigillose; corolla white, 5-merous, the lobes ovate, 1–1.6 mm long, the tube 3.5–5.3 mm long, strigillose outside; stamens 5, the anthers lanceoloid, 1.1–1.3 mm long, sessile, inserted beneath the middle of the corolla tube; ovary globose, 0.8–1 mm long, the disc scarcely evident, the stigma nearly sessile, capitate. Fruits white, ovoid, 3–4 mm long, strigillose.

Distribution. *Tournefortia hirsutissima* is found in diverse habitats from sea level to 2,000 m in elevation, and is ubiquitous throughout the Neotropics. In Panama, it is known from the Canal Area, Chiriquí, Darién, Panamá, and San Blas.

Tournefortia hirsutissima is one of the

most commonly collected members of the genus and appears to be most closely related to *T. bicolor* (discussion under that species). The two can be distinguished most easily by the usually strigose upper leaf surface in *T. hirsutissima*, while it is glabrous or nearly so in *T. bicolor*. One collection from Darién (Stern 501) is unique in having a white abaxial leaf surface, but it otherwise fits well within *T. hirsutissima*, agreeing in all other aspects.

Additional specimens examined. PANAMA. CANAL AREA: forest reserve, near crossing of Cruces trail and Madden Dam road, *Bartlett & Lasser 16348* (GH, MO); Juan Mina, *Bartlett & Lasser 16529* (GH, MO); Barro Colorado Island, *Croat 4797, 6246, 10750A, 11718* (MO); roadside W of Gatún Locks, *Croat 12432* (MO); vicinity of Fort San Lorenzo, *Croat 12521* (MO); Barro Colorado Island, *Croat 15054* (MO); along road between Gatún Locks and Ft. Sherman, *Croat 15380* (MO); hill above Thatcher-Ferry Bridge, *Croat 17014* (MO); Fort Sherman, *Dwyer & Robyns 172* (MO); *Dwyer 6685* (MO); Madden Dam, Boy Scout Camp Road, *Dwyer & Elias 7513* (MO); Gatún Station, *Hayes 61* (GH); vicinity of Río Chagres Bridge, road leading to abandoned weather post, ca. 2 km by road SE of Gamboa along highway to Balboa, *Lasseigne 4271* (MO); west side of Ferry Thatcher Bridge, along mangrove margin, *Lazor 2881* (MO); Pipeline Road, *Meijer 160* (MO); Pipeline Road, 10–15 mi. from Gamboa, 100 m, *Miller 1027* (MO); along road from Fort Sherman to Fort San Lorenzo, *Porter et al. 4984* (MO); vicinity of Madden Dam, near Río Chagres, 50–75 m, *Seibert 560* (MO); Barro Colorado Island, *Shattuck 970* (MO (3)); *Starry 238* (MO); Fort Sherman near mouth of Chagres River, *Tyson 1535* (MO); Old Fort San Lorenzo, *Tyson 1571, 1572* (MO); *Tyson & Blum 3698* (GH, MO); Barro Colorado Island, *Wilson 44* (MO). CHIRIQUÍ: Llanos on slopes of Volcán de Chiriquí Viejo and along Río Chiriquí Viejo, 1,200 m, *Allen 968* (MO); Boquete, lumber road into the hills east of the Río Caldera, 4,500–6,500 ft., *Allen 4654* (GH, MO); Burica Peninsula, Quebrada Manzanillo, 9 km SSW of Puerto Armuelles, *Busey 746* (MO); 1 mi. W of airport at Puerto Armuelles, *Croat 21905* (MO); Puerto Limónes, along coast near the beach, *Croat 22119* (MO); Burica Peninsula, Distrito Guanabano, disturbed areas along Quebrada Guanabano, 0–100 m, *Croat 22534* (MO); San Bartolo Arriba W of Puerto Armuelles, *Croat 26700* (MO); Las Lagunas area W of Hato del Volcán, 1,400 m, *Hamilton & Stockwell 3562* (MO); Burica Peninsula, 2.5 km W of Puerto Armuelles, 80 m, *Liesner 16* (MO); Burica Peninsula, Quebrada Merica, 4 mi. S of Puerto Armuelles, 0–100 m, *Liesner 384* (MO); along road 3–5 mi. NW of El Hato del Volcán towards Costa Rica across the Río Chiriquí Viejo, 3,000–4,000 ft., *Luteyn 859* (MO); valley of the upper Río Gariche, 1,050–1,100 m, *Seibert 357* (GH, MO). COLÓN: 4 mi. W of Portobelo, near sea level, *Antonio 1764* (MO); Portobelo, *Billberg 269* (GH); Isla Grande, *D'Arcy 4033B* (MO); Portobelo, *Dwyer 5146* (GH); La Guayra, E of Portobelo, *Knapp & Mallet 5725* (MO). DARIÉN: headwaters of Río Chico,

500–750 ft., *Allen 4638* (GH); vicinity of Caña, 1,750 ft., *Stern et al. 501* (GH). PANAMÁ: a orillas de la carretera hacia Pacora 1 km despues del Autodromo Panamá, *Carrasquilla 191* (MO); a 4 km del corregimiento de Pacora, *Carrera 19* (MO); vicinity of Macambo, *Croat 14906A* (MO); Cerro Azul, *Dwyer 1876* (MO); Tocumen, *Dwyer 4056* (MO (2)); Las Guacas, población a orillas del Río Chagres, *Kant 39* (MO); El Llano–Carti Road, 18 km from Interamerican Highway, 350 m, *Mori et al. 4582* (MO); El Llano–Carti Road 17.5 km from Interamerican Highway, 350 m, *Mori et al. 4623* (MO); road to Cerro Campana, 10 km from Interamerican Highway, 300 m, *Sullivan 438* (MO); between Chepo and La Capitana, *Tyson 6758* (MO (2)); wet savanna E of Pacora, *Woodson et al. 721* (GH (2)). SAN BLAS: through cultivation on mainland in front of Ustupo, *D'Arcy 9507* (MO).

Tournefortia johnstonii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 991. 1938. TYPE: Costa Rica. Heredia: Cerro de las Caricias, north of San Isidro, 2,000–2,400 m, *P. C. Standley & J. Valerio 52087* (holotype, US 1306982).

Shrub to 3 m tall, or rarely a small tree to 6 m tall, the twigs velutinous. Leaves opposite, the lateral buds usually with small expanding leaves with appearance of stipules; petioles 9–30(–40) mm long, velutinous; leaf blade lanceolate to ovate, (7.8–)10–18(–23) cm long, (3–)4–8(–10) cm wide, the apex acuminate, the base cuneate to acute, the margin entire to unevenly undulate, the adaxial surface velutinous, the abaxial surface velutinous, the secondary veins 10–12, the tertiary and quaternary veins clearly evident. Inflorescence terminal, a once- or rarely twice-branched cyme, the branches (2.5–)4–15 cm long, the peduncle (3–)5–12 cm long, velutinous. Flowers bisexual, sessile, borne 1–5 (–7) mm apart; sepals 5, lanceolate, 6–10.5 mm long, strigillose to strigose; corolla tubular with spreading lobes, white to green, 5-merous, the lobes lance-ovate to ovate, the apex acuminate, 2.6–5 mm long, the tube 8–10 mm long, strigillose, at least near the apex; stamens 5, the anthers lanceoloid, 1.5–2 mm long, sessile, inserted just below the mouth of the corolla tube; ovary ovoid, 0.8–1 mm long, the disc scarcely evident, the style 3–3.5 mm long, the stigma conical. Fruits white, ovoid, 4.5–7 mm long, separating into 2–4 nutlets at maturity.

Distribution. *Tournefortia johnstonii* occurs only in Panama and Costa Rica in cloud forests at elevations of 1,000–3,000 m. In Panama it is known only from the provinces of Chiriquí and Veraguas.

Tournefortia johnstonii is very similar in general aspect to *T. ramonensis* but differs in being a smaller plant with longer, coarser indument on the twigs. Also, the lower leaf surfaces of *T. johnstonii* are usually darker in color after drying.

Additional specimens examined. PANAMA. CHIRIQUÍ: Cerro Colorado, near continental divide, 1,500 m, *Antonio 1459* (MO); along road between Cerro Punta and Las Nubes, 1,800–2,100 m, *Croat 26391* (MO); Las Nubes, 2,000 m, *Croat 26456* (MO); E of Boquete along steep, forested slopes and in wooded pastures on Cerro Azul near Quebrada Jaramillo, 1,620–1,700 m, *Croat 26867* (MO); Alto Respinga and above, 2,800 m, *D'Arcy 9991* (MO); mountain directly S of Cerro Respinga, *D'Arcy 10811* (MO); E slope of Volcán de Chiriquí (Baru), above Boquete, along road in oak forest, 2,600 m, *Davidse & D'Arcy 10264* (MO); Volcán de Chiriquí, 9,000 ft., *Davidson 976* (GH, MO); along Boquete trail, Cerro Respinga, 2,000–2,500 m, *Gentry 5978, 6013* (MO); path above Cerro Punta to Boquete, 2,500 m, *Hamilton & Stockwell 3417* (MO); *Hamilton & Krager 3741* (MO); 7 km NW of Cerro Punta, 7,200 ft., *Hammel 1472* (MO); Cerro Hornito, 5,600 ft., *Hammel 3043* (MO); Quebrada Alemán, 8 mi. N of Los Planes de Hornito I.R.H.E. Fortuna Hydroelectric Project, 1,200 m, *Knapp et al. 4155* (MO); trail from Cerro Punta to Boquete, 2,160–2,260 m, *McDaniels 10255* (MO); N of San Felix at Chiriquí–Bocas del Toro border, on Cerro Colorado copper mine road along continental divide, 5,000–5,500 ft., *Mori & Kallunki 5939* (MO); 3.7 km E of bridge NE of Cerro Punta on road through Bajo Grande, 2,250–2,400 m, *Stevens 18199* (MO); 3.7 km along road through Bajo Grande from bridge NE of Cerro Punta, 2,250–2,400 m, *Sytsma & Stevens 2143* (MO); along the trail between Cerro Punta and the Quebrado Bajo Grande, 2,000–2,100 m, *Wilbur et al. 11903* (MO); thickets along trail between Las Mirandas and Las Nubes and a small valley running NW of the mountain of Cerro Punta about 3 mi. from village of Cerro Punta, *Wilbur & Teeri 13271* (GH, MO); vicinity of Casita Alta, Volcán de Chiriquí, 1,500–2,000 m, *Woodson et al. 888* (GH, MO). VERAGUAS: Cerro Tute, E slopes, 1 km beyond Escuela Agrícola Alto Piedra above Santa Fe, 1,200–1,450 m, *Sytsma & Anderson 4593* (MO).

Tournefortia longispica James S. Miller, sp. nov. TYPE: Panama. Bocas del Toro: road from Fortuna Dam to Chiriquí Grande, 3.1 mi. N of continental divide, 700 m, disturbed primary forest, G.

McPherson 6778 (holotype, MO 3386969). Figure 6.

Suffrutex ad 2 m altus, ramulis glabris. Folia alterna; petioli (1.5–)2.5–4(–6.5) cm longi; lamina elliptica ad oblonga, (14–)17–25 cm longa, (5.5–)6.5–9(–10.5) cm lata, apice acuminata, basi acuta ad attenuata, glabra. Inflorescentia terminalis, cyma ramorum duorum, ad 30 cm longorum post anthesin composita, pedunculo 10–22 cm longo, glabro vel fere glabro. Flores sessiles, 1–5 mm distantibus; sepala lanceolata, 2.5–3 mm longa; corolla alba ad pallido-viridis, tubularis, lobis patulis, ovatis ad late ovatis, 2–2.5 mm longis, tubo extus strigilloso; antheris 1.5–2 mm longis, sessilibus, ad medium tubi insertis; stylus 0.6–1 mm longus, stigmati conoidei. Fructus globosi ad valde lato-ovoidei, 6–9 mm longi, 9–12 mm lati, glabri, laeves.

Shrub to 2 m tall, the twigs glabrous. Leaves alternate; the petioles (1.5–)2.5–4(–6.5) cm long, glabrous or nearly so; leaf blade elliptic to oblong, (14–)17–25 cm long, (5.5–)6.5–9(–10.5) cm wide, the apex acuminate, the base acute to attenuate, the margin entire, the adaxial surface glabrous, the abaxial surface glabrous but with very small appressed hairs along the major veins, the secondary veins 8–11, the tertiary veins evident, the quaternary veins often obscure. Inflorescence terminal or subterminal, usually a twice-branched cyme, the branches elongate, to 30 cm long at fruiting, the peduncle 10–22 cm long, glabrous to shortly brown puberulent or strigillose. Flowers sessile, bisexual, borne 1–5 mm apart; sepals 5, lanceolate, 2.5–3 mm long, sparsely to evenly strigillose; corolla tubular with spreading lobes, white to pale green, 5-merous, the lobes ovate to widely ovate, 2–2.5 mm long, the tube 4–5.5 mm long, strigillose outside; stamens 5, the anthers lanceoloid, 1.5–2 mm long, sessile, inserted in the middle of the corolla tube; ovary ovoid, 0.8–1 mm long, the disc crateriform or barely evident, the style 0.6–1 mm long, the stigma conical. Fruits white, globose to very broadly ovoid, 6–9 mm long, 9–12 mm broad, glabrous, smooth.

Distribution. *Tournefortia longispica* is known only from Panama from the provinces of Bocas del Toro, Chiriquí, Coclé, and Veraguas, where it occurs in cloud forests at elevations of 600–1,500 m.

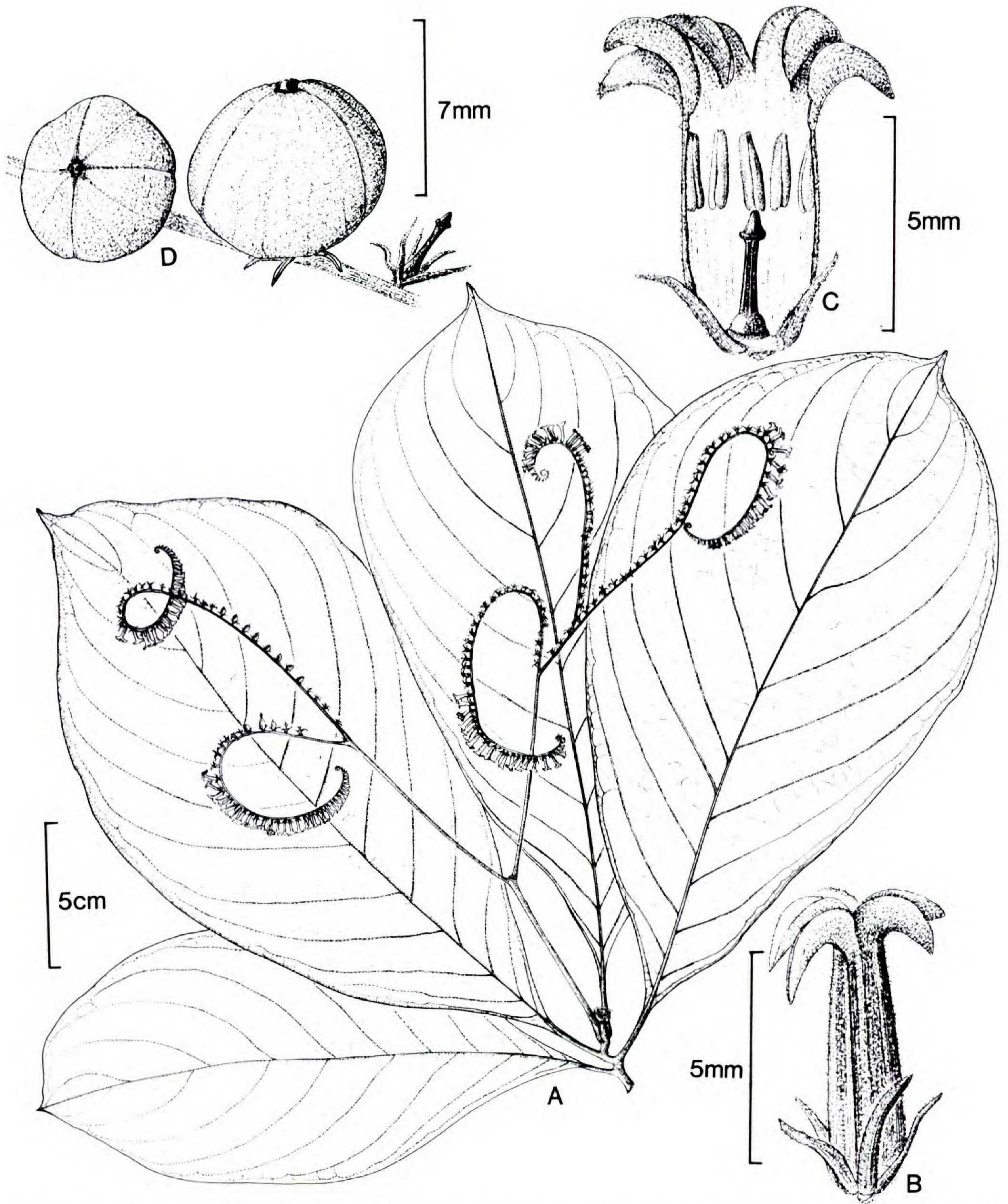


FIGURE 6. *Tournefortia longispica*.—A. Flowering branch.—B. Flower.—C. Flower with corolla opened.—D. Fruits. A–C from McPherson 6778 (MO), Bocas del Toro, Panama; D from McPherson 7247 (MO), Bocas del Toro, Panama.

Tournefortia longispica is distinct within the genus in having an elongate, dichotomously branched inflorescence and large, nearly glabrous leaves. It has no known close relatives in Panama but could be confused with *T. glabra*, which differs in having a much-branched inflorescence. Several of the

collections have large, swollen fruits apparently parasitized by insects, a common condition in the genus.

Additional specimens examined. PANAMA. BOCAS DEL TORO: E slope of La Zorra to divide, Kirkbride & Duke 824 (MO); in forest along trail down hill from Finca Serrano, 4,600 ft., Hammel 6166 (MO); along trail on

divide separating Chiriquí and Bocas del Toro, 1,150 m, *McPherson 7247* (MO). CHIRIQUÍ: Fortuna Dam area to N of reservoir near Quebrada Bonito, 1,100 m, *Churchill 5811* (MO); W side of Río Hornito, 1,100–1,300 m, *D'Arcy 16009* (MO). COCLÉ: El Copé on Pacific side ½ hour walk from sawmill, *Antonio 2109* (MO); Cerro Pilón, El Valle, 3,000 ft., *Duke & Lallathin 14962* (MO); Cerro Pilón, 2,900 ft., *Dwyer & Lallathin 8687* (MO); El Valle, *Folsom 2658* (MO); New Works at Rivera sawmill, Alto Calvario, 600–800 m, *Folsom 3164* (MO); Cerro Pilón, 900–1,173 m, *Liesner 786* (MO). VERAGUAS: Ridge of Cordillera de Tute, trail to Cerro Tute, above Escuela Agrícola Alto de Piedra, just W of Santa Fe, 800–1,350 m, *Knapp & Dressler 5425* (MO).

***Tournefortia maculata* Jacq., Enum. Syst. Pl. 14. 1760; Select. Stirp. Amer. Hist. 47. 1763.** TYPE: Colombia, Bolívar: Cartagena (not seen).

Woody climbing vine, the twigs sparsely strigillose, later glabrous. Leaves alternate; petioles (3–)5–12 mm long, sparsely short-strigillose; leaf blade (3–)5–9 cm long, (1.5–)2.5–4 cm wide, the apex acuminate to attenuate, the base acute to obtuse and often slightly decurrent, the margin entire, the adaxial surface very sparsely short-strigillose, the abaxial surface evenly short-strigillose. Inflorescence usually terminal, a loose, much-branched cyme, the branches to 5 cm long, the peduncles 18–24 mm long, puberulent to strigillose. Flowers sessile, borne 1–10 mm apart, bisexual; sepals lanceolate to triangular, 0.8–2 mm long, strigillose; corolla pale yellow-green, 5-merous, the lobes filiform, 1.5–3 mm long, the tube 3.3–5 mm long, densely strigillose; stamens 5, the anthers lanceoid, 0.8–1 mm long, connate apically, nearly sessile, inserted in the mouth of the corolla tube; ovary ovoid, 0.8–1 mm long, the disc crateriform to scarcely evident, the style 0.8–4 mm long, the stigma capitate. Fruits 4-lobed, 2.5–4 mm long, glabrous, white with black markings.

Distribution. *Tournefortia maculata* ranges from Mexico to South America and the West Indies and is found in a wide variety of habitats from sea level to 1,500 m in elevation. In Panama it is known from most provinces and probably occurs in all of them.

Tournefortia maculata is distinctive, with its four-lobed fruits and glabrous leaves. The only other Central American *Tournefortia* with four-lobed fruit is *T. volubilis*, which differs in having sericeous leaves. These two belong to sect. *Cyphocyema* I. M. Johnston, a complex group of species centered in South America and characterized by four-lobed fruits and apically connate anthers.

Additional specimens examined. PANAMA. CANAL AREA: Río Abajo, *Bartlett & Lasser 16398* (GH, MO); low woods E of Bella Vista, a suburb of Panama City, *Maxon & Valentine 6942* (GH); Fort San Lorenzo, Fort Sherman Military Reservation, *Maxon & Valentine 7011* (GH); vicinity of Salamanca Hydrographic Station, Río Pequeni, 80 m, *Woodson et al. 1630* (GH, MO). CHIRIQUÍ: Boquete, 4,000 ft., *Davidson 853* (MO); Bajo Mona, mouth of Quebrada Chiquara, along Río Caldera, 1,500–2,000 m, *Woodson 1007* (GH). COCLÉ: between Las Margaritas and El Valles, *Woodson et al. 1279* (GH, MO). COLÓN: Santa Rita Ridge Road, 4 mi. from Transisthmian Highway to Agua Clara weather station, 500 m, *Gentry et al. 8835* (MO (2)); Santa Rita Ridge, ca. 5.5–6 mi. E of Transisthmian Highway, *Lewis et al. 5387* (MO); along Río Viejo, between the Portobelo Road and Quebrada Ruíz, 4 km NE of Puerto Pilón, 5 m, *Nee 7171* (MO). DARIÉN: Río Tuqueza below Quebrada Venado, *Bristan 1076* (MO); Cerro Pirre, 2,500–4,500 ft., *Duke & Elias 13665* (MO). LOS SANTOS: Loma Prieta, 800–900 m, *Duke 11879* (MO); Poci, *Dwyer 1193* (MO); Guarare, *Dwyer 2469* (MO); Loma Prieta, Cerro Grande, 2,400–2,800 ft., *Lewis et al. 2241* (MO). PANAMÁ: Cerro Azul, Goofy Lake, *Dwyer 2412* (MO); San José Island, *Erlanson 114, 150, 241, 249, 379, 388, 501* (GH); Taboga Island, 0–25 m, *Pittier 3536* (GH); Cerro Jefe, 850–900 m, *Sytsma 1979* (MO); on road from Chepo to El Llano, *Tyson & Smith 4119* (MO), Isla Taboga, 0–186 m, *Woodson et al. 1474* (GH, MO). SAN BLAS: to Udirbi, El Llano–Carti Road, 200–350 m, *D'Arcy et al. 16037* (MO). VERAGUAS: along road between Santa Fe and Escuela Agrícola Alto Piedra, 600–800 m, *Croat 26007* (GH, MO); Río de Jesús, *Dwyer 339* (MO); Isla de Coiba (Penal Colony), *Dwyer 2330* (MO); 5 mi. E of Santiago, *Tyson et al. 4284* (MO).

***Tournefortia multiflora* James S. Miller, sp. nov.** TYPE: Panama. Veraguas: NW of Santa Fe, 8.8 km from Escuela Agrícola Alto de Piedra, on road to Calovebora, elev. 1,900 ft., *S. Mori 6659* (holotype, MO 3386967). Figure 7.

Frutex vel arbor parva ad 5 m alta, ramulis glabris. Folia alterna sed saepe prope apices caulis conferta, paene sessilia vel in petiolis ad 2(–7) cm longis, suffultis; lamina elliptica, 16–50 cm longa, 8–18 cm lata, apice obtuso ad rotundato et saepe abrupta brevi-acuminato, base attenuata quasi glabra. Inflorescentia terminalis, paniculata,

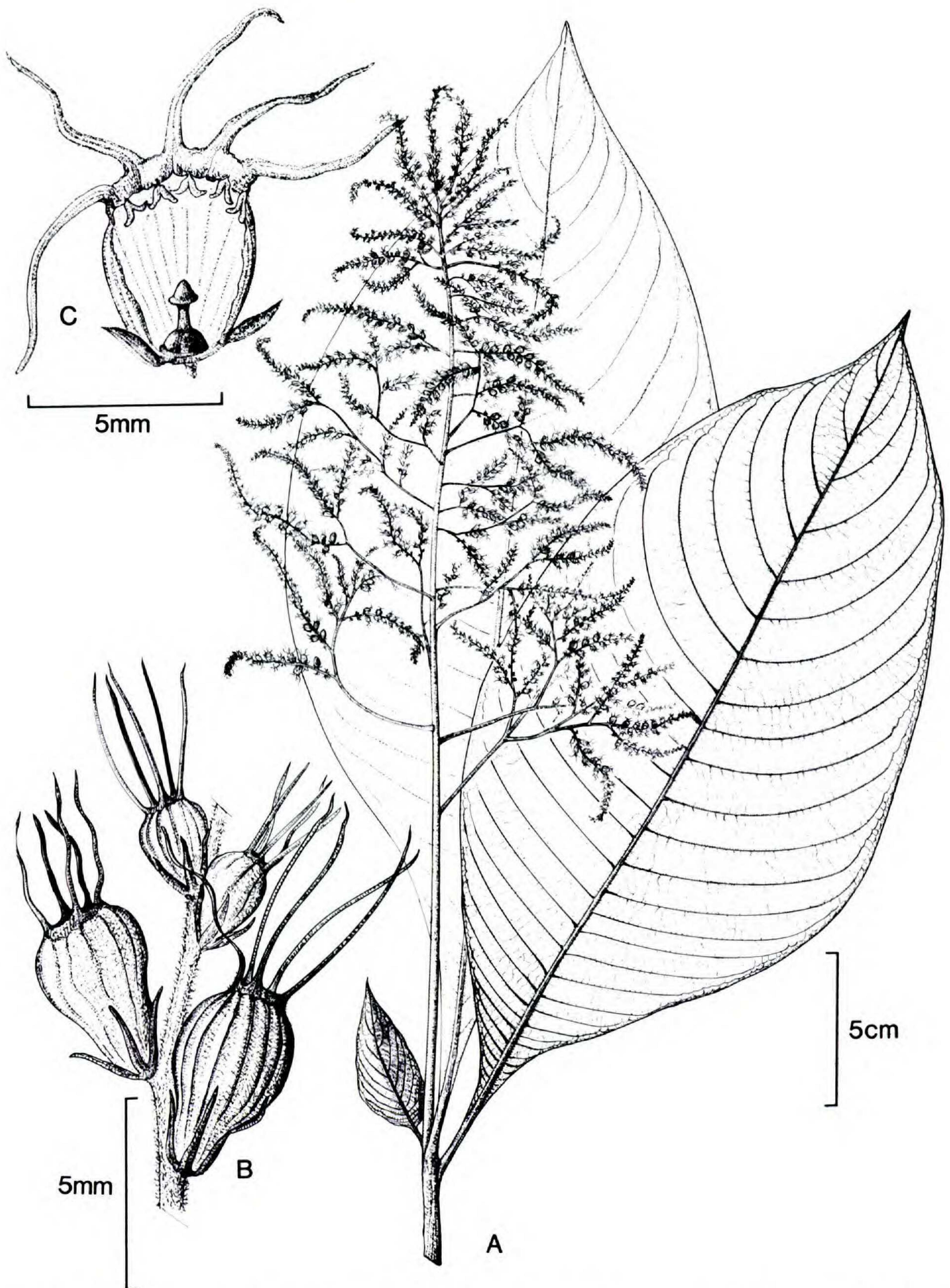


FIGURE 7. *Tournefortia multiflora*.—A. Flowering branch.—B. Flowers.—C. Flower with corolla opened showing pendent anthers. From Mori 6659 (MO), Veraguas, Panama.

20–40 cm longa, 16–30 cm lata, pedunculo 10–19 cm longo, fusco-puberulo. Flores sessiles, seorsum 2–5 mm dispositi; sepala 5, lanceolata, 1.7–3.2 mm longa; corolla viridi-alba, striis atroviridibus ornata, urceolata lobis patulis, pentameris, lobis linearibus, 3–4.5 mm longis, tubo 3.5–5 mm longo, extus puberulo; stamina 5, antheris conspicua bilobatis et in ore corollae tube pendentibus, 0.5–0.8 mm longis; stylus 0.5–1.6 mm longus, stigmatibus

conoidi, puberulo. Fructus albi, ovoidei, 4.5–5.5 mm longi, 3–4 mm lati, glabro.

Shrub or small tree to 5 m tall, the twigs glabrous. Leaves alternate but often crowded near the stem apices, nearly sessile or on petioles to 2(–7) cm long; blade elliptic, 16–

50 cm long, 8–18 cm wide, the apex obtuse to rounded and often abruptly short-acuminate, the base attenuate, the margin entire, the adaxial surface essentially glabrous with widely scattered, short, appressed hairs, the abaxial surface glabrous, strigillose along the midrib and the 15–22 arcuate secondary veins, the tertiary and quaternary veins clearly evident. Inflorescence terminal, paniculate, 20–40 cm long, 16–30 cm broad, the peduncle 10–19 cm long, the peduncle and branches brown-puberulent. Flowers sessile, borne 2–5 mm apart; sepals lanceolate, 1.7–3.2 mm long, puberulent or strigillose to glabrous; corolla urceolate with spreading lobes, greenish white with darker green stripes, the lobes linear, 3–4.5 mm long, the tube 3.5–5 mm long, puberulent outside; stamens 5, the anthers distinctly bilobed and pendent in the mouth of the corolla tube, 0.5–0.8 mm long; ovary globose, 0.5–0.9 mm long, the disc crateriform, the style 0.5–1.6 mm long, the stigma conical, puberulent. Fruits ovoid, white, 4.5–5.5 mm long, 3–4 mm broad, glabrous.

Distribution. *Tournefortia multiflora* is known only from Panama, where it occurs in wet forest in the provinces of Veraguas and Colón from 400–900 m in elevation.

Tournefortia multiflora is distinctive with its large leaves to 50 cm long and unique in the genus in its large, many-flowered inflorescence, unusual striped flowers with linear corolla lobes, pendent anthers, and puberulent stigma. Despite these distinctions, it does have a gynoeceium with a conical stigma and the two-lobed fruits that characterize the genus. It also has pollen grains that are similar to the majority of other species of *Tournefortia* (Nowicke & Miller, unpubl.). Johnston (1954) noted that pollen morphology seems to be a valuable generic character in the Boraginaceae, and, although unique in some characters, *T. multiflora* clearly falls within the morphological and palynological boundaries of the genus.

Additional specimens examined. PANAMA. COLÓN: Santa Rita Ridge trail, beyond end of Santa Rita Ridge

Road (Panamanian Highway (R20D)), 17–35 km from Boyd–Roosevelt Highway, 400–800 m, *Mori & Crosby 6413* (MO). VERAGUAS: along Río Primero Braso, *Croat 25976* (MO); N of Santa Fe, 6.5 km from Escuela Agrícola Alto de Piedra, *Mori & Kallunki 3067* (MO).

Tournefortia ramonensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 992. 1938. TYPE: Costa Rica. Alajuela: Los Angeles de San Ramón, Apr. 1928, *Brenes 6118* (holotype, F 851176; isotype, NY).

Shrub to 3 m tall, the twigs densely puberulent. Leaves opposite; petioles 13–28 mm long, densely puberulent; leaf blades widely ovate to lance-ovate, 8.9–15 cm long, 3.5–9 cm wide, the apex acuminate, the base acute and decurrent, the margin entire to unevenly dentate, the adaxial surface sparsely strigillose, the abaxial surface sparsely pubescent, lighter in color than above, the tertiary and quaternary veins clearly visible. Inflorescence terminal or axillary, a once- or twice-branched cyme, the branches 3–7.5 mm long, the peduncle 6–9 cm long, brown puberulent. Flowers sessile, borne 2–4 mm apart, bisexual; sepals lanceolate, ca. 6 mm long, strigillose; corolla tubular with spreading lobes, greenish white, the lobes ovate, 2 mm long, the tube 9.5 mm long, puberulent outside; ovary ovoid, 1 mm long, the disc crateriform, the style 4 mm long, the stigma pyramidal. Fruits broadly ovoid, white, 4–5 mm long, 3–4.5 mm broad, glabrous, the style often persisting.

Distribution. *Tournefortia ramonensis* is known only from high elevations in cloud forests in Costa Rica and the provinces of Bocas del Toro and Chiriquí in Panama.

Tournefortia ramonensis is distinctive in being one of only two Panamanian members of the genus with opposite leaves. The other, *T. johnstonii*, is a low shrub rather than a tree and has coarse velutinous twigs compared with the puberulent twigs of *T. ramonensis*.

Additional specimens examined. PANAMA. BOCAS DEL TORO: Robalo Trail, northern slopes of Cerro Horqueta,

6,000–7,000 ft., *Allen 4919* (GH, MO). CHIRIQUÍ: vicinity of Bajo Chorro, 1,900 m, *Woodson & Schery 609* (GH (2), MO).

Tournefortia tacarcunensis A. Gentry & Nowicke, *Ann. Missouri Bot. Gard.* 64: 134. 1977. TYPE: Panama. Darién: Cerro Tacarcuna, west ridge, trail from summit camp to waterfall east of camp, 1,550–1,700 m, *A. H. Gentry & S. Mori 14114* (holotype, MO 2280271).

Low subshrub to 0.5 m tall, the twigs glabrous or nearly so. Leaves alternate; petioles 2–3 mm long, glabrous or nearly so; leaf blade elliptic to elliptic-ovate, 8.3–23 cm long, 3.2–8 cm wide, the apex acuminate, the base cuneate, the margin entire to unevenly undulate, the adaxial surface glabrous, the abaxial surface glabrous, much lighter than above, tertiary and quaternary veins obscure. Inflorescence terminal, a once- or twice-branched dichotomous cyme, the peduncle 2–6 cm long, brown-strigillose. Flowers borne 2–3 mm apart, bisexual; sepals lanceolate, 3.5–4.5 mm long, sparsely brown-puberulent; corolla tubular, white or greenish white, the lobes spreading, very widely ovate, rounded at the apex, 2–2.2 mm long, the tube 9–9.5 mm long; stamens 5, the anthers ovoid to lanceoloid, 1.3–1.5 mm long, sessile, inserted just below the mouth of the corolla tube; ovary globose to ovoid, 1–1.7 mm long, the disc scarcely evident, the style 6–7 mm long, the stigma conical. Fruits broadly ovoid, white, 4–6 mm long, 4–5.5 mm broad, glabrous.

Distribution. *Tournefortia tacarcunensis* is known only from Darién in Panama and Valle in Colombia in cloud forests of the Serranía del Darién above 1,500 m in elevation.

Tournefortia tacarcunensis is poorly understood, being known from only the type and a collection from adjacent Colombia, both from Cerro Tacarcuna. While it appears to be endemic in this region, this is one of the most poorly known areas of both Panama and Colombia.

Tournefortia urceolata James S. Miller, sp. nov. TYPE: Panama. Bocas del To-

ro: along continental divide from road branching N off main Fortuna–Chiriquí Grande Highway near continental divide, 1.1 mi. from main highway, ca. 1,200 m, *T. B. Croat & M. H. Grayum 60301* (holotype, MO 3386968). Figure 8.

Frutex ad 2 m altus, ramulis glabris vel fere glabris. Folia alterna, petiolis 8–32 mm longis; lamina lanceolata vel angusto-elliptica ad elliptica, (10.7–)13.5–31(–38) cm longa, (3.2–)4–14(–17.5) cm lata, apice acuminata, basi attenuata, glabris vel fere glabra. Inflorescentia terminalis, pyramidalis cymis parvis praedita, 13–28 cm longa, pedunculo (5–)9–21 cm longo. Flores sessiles vel in pedunculis brevibus ad 1 mm longis, seorsum 1–3 mm dispositis; sepala lanceolata, 3.5–5 mm longa; corolla viridis ad viridi-flava, tubularis ad urceolata lobis patulis, lanceolatis, 3–4 mm longis; antheris 1–2 mm longis, sessilibus, infra faucem fere ad medium corollae tubi insertis; stylus 1.7–2.5 mm longus, stigmatе spinulo ad puberulo. Fructus late ovoidei, albi, 4–6 mm longi, 4–6 mm lati, glabri.

Shrub to 2 m tall, the twigs glabrous to brown puberulent. Leaves alternate; petioles 8–32 mm long, glabrous to brown-puberulent, the blade lanceolate or narrowly elliptic to elliptic, (10.7–)13.5–31(–38) cm long, (3.2–)4–14(–17.5) cm wide, the apex acuminate, the base attenuate, the margin entire, the adaxial surface glabrous, the abaxial surface essentially glabrous, strigillose along the major veins and papillose between them, the secondary veins 9–15, the tertiary and quaternary veins clearly evident. Inflorescence terminal, pyramidal, a panicle of small cymes, 13–28 cm long, the peduncle (5–)9–21 cm long, brown strigillose to puberulent. Flowers sessile or on short petioles to 1 mm long, borne 1–3 mm apart; sepals 5, lanceolate, 3.5–5 mm long, sparsely to evenly strigillose; corolla green to greenish yellow, tubular to urceolate with spreading lobes, 5-merous, the lobes lanceolate, 3–4 mm long, the tube 7–10 mm long, strigillose outside; stamens 5, the anthers lanceoloid, 1–2 mm long, sessile, inserted from just below the mouth to just above the middle of the corolla tube; ovary ovoid, 0.5–0.8 mm long, the disc scarcely evident to crateriform, the style 1.7–2.5 mm long, the stigma conical, spinulose to puberulent. Fruits broadly ovoid, white, 4–6 mm long, 4–6 mm broad, glabrous.

Distribution. *Tournefortia urceolata* is

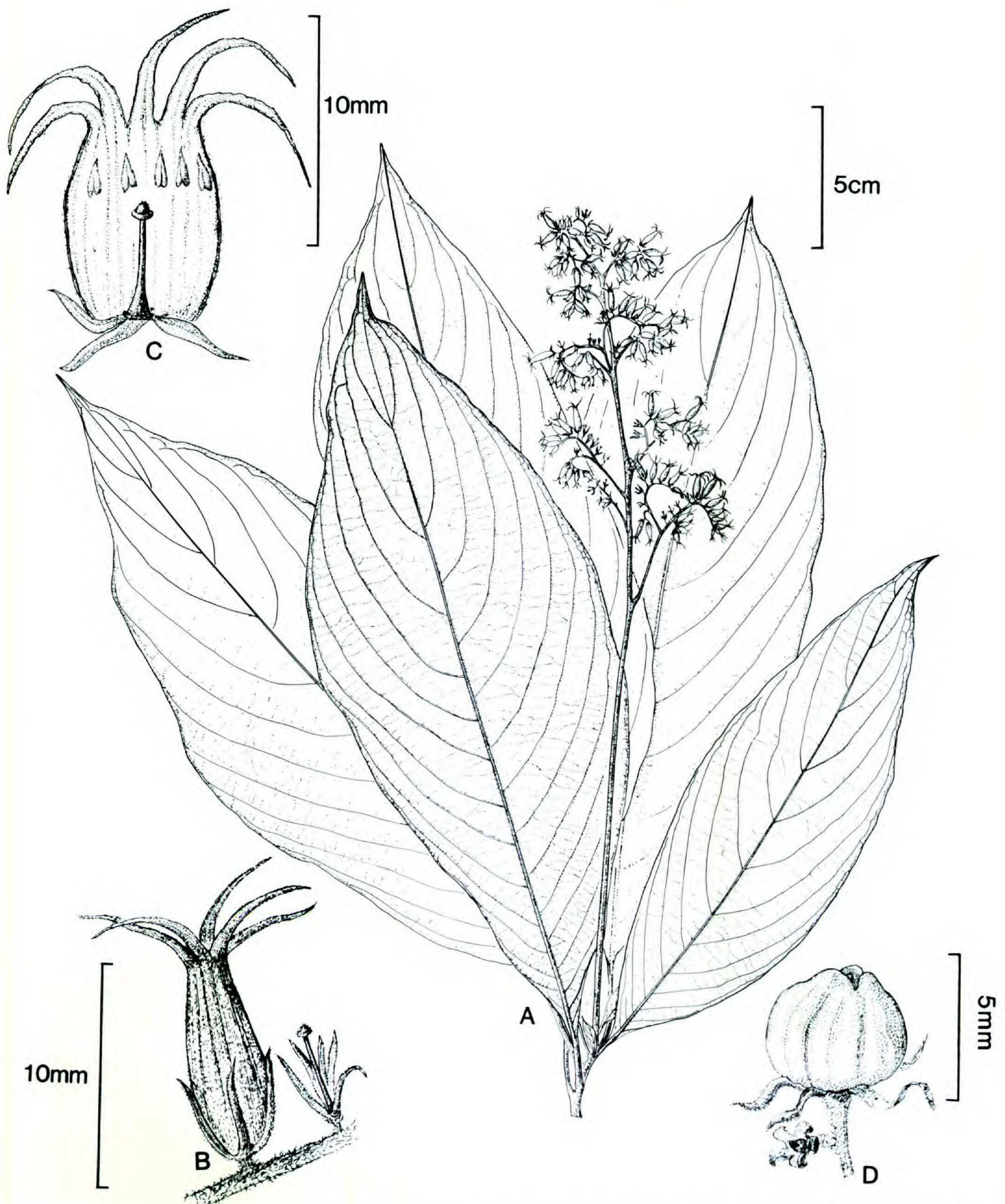


FIGURE 8. *Tournefortia urceolata*.—A. Flowering branch.—B. Flower.—C. Flower with corolla opened.—D. Fruit. A–C from Croat & Grayum 60301 (MO), Bocas del Toro, Panama; D from Croat 37301 (MO).

known only from Panamá in Chiriquí, Colón, and San Blas, where it occurs in cloud forests at elevations of 400–2,300 m.

Tournefortia urceolata is distinct in its large glabrous leaves with relatively obscure venation and urceolate corollas. Vegetatively it somewhat resembles *T. glabra* but can be

distinguished by its less prominent tertiary veins, sepals longer than 3 mm, and corolla longer than 7 mm.

Additional specimens examined. PANAMA. CHIRIQUÍ: Fortuna Dam area, on Kaolin hill, just N of reservoir, 1,100–1,400 m, *D'Arcy et al.* 15919 (MO); forested slopes below divide ridge near Cerro Pate Macho, 6,200 ft., *Hammel* 5817 (MO); Palo Alto, 4.5 mi. NE of Bo-

quete, forest along western branch of headwaters of Río Palo Alto, 6,300 ft., *Hammel 7414* (MO); S slopes of Cerro Pate Macho, along Río Palo Alto, 1,300–1,800 m, *Knapp et al. 2077* (MO); ca. 0.5 km E of Cerro Pate Macho, headwaters of Río Palo Alto, 1,800–2,100 m, *Knapp et al. 2121* (MO); SE slopes and summit of Cerro Pate Macho, trail from Río Palo Alto, 4 km NE of Boquete, 1,700–2,100 m, *Sytsma et al. 4845* (MO). COLÓN: on Santa Rita Ridge Road, 17–35 km from Boyd–Roosevelt Highway, 400–800 m, *Mori & Crosby 6413* (MO). SAN BLAS: Cerro Brewster, headwaters of Río Cangandí, 2,300 ft., *De Nevers et al. 5500* (MO).

***Tournefortia volubilis* L., Sp. Pl. 140.**

1753. TYPE: without locality or collector (holotype, LINN (Savage Catalog number 193.3), not seen; microfiche, MO).

Tournefortia floribunda Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 79. 1818. TYPE: Venezuela. Sucre: prope Cumaná (holotype, B-WILLD, not seen; microfiche, MO).

Tournefortia velutina Kunth in Humb., Bonpl. & Kunth, Nov. Gen. Sp. 3: 79, t. 201. 1818. TYPE: Mexico. Guerrero: Acapulco, collector unknown 3863 (holotype, P, not seen; microfiche, MO).

Tournefortia potosina Standley, Contr. U. S. Natl. Herb. 23: 1230. 1924. TYPE: Mexico, San Luis Potosí: Tamasopo Canyon, 750 m, *C. G. Pringle 3518* (holotype, US 316801; isotype, CAS).

Woody vine or occasionally a small shrub, the twigs densely puberulent. Leaves alternate; petioles 4–8(–12) mm long, densely puberulent; leaf blade lanceolate to lance-ovate, (2.7–)5–7(–10.4) cm long, (1–)2–3.5(–5) cm wide, the apex acuminate, the base obtuse to rounded, the margin entire, the adaxial surface strigillose, the abaxial surface densely puberulent to nearly tomentose. Inflorescence terminal or internodal, a loosely branched cyme, the peduncle 3–16 mm long, the fertile branches 3–5(–10) cm long. Flowers sessile, borne 1–5 mm apart; sepals linear-lanceolate, 1.2–1.8 mm long, densely strigillose; corolla dull yellow or white to pale green, the lobes linear-lanceolate, ca. 1.5 mm long, the tube 2–2.3 mm long, densely strigillose outside; stamens 5, the anthers ovoid, 0.5–0.7 mm long, connate apically, sessile, inserted near mouth of corolla tube; ovary ovoid, 0.6–0.8 mm long, the stigma conical, exceeding the calyx lobes, elongate. Fruits distinctly 4-lobed, 2–3 mm long, glabrous, white with dark brown to black spots at the apex.

Distribution. *Tournefortia volubilis* is widely distributed in dry, disturbed areas from sea level to 600 m in elevation from Mexico throughout Central America to Panama, and is found in the West Indies. In Panama it is known only from the provinces of Los Santos and Panamá.

Tournefortia volubilis is a member of the complex sect. *Cyphocyema* I. M. Johnston, a group centered in South America. It differs from the only other Central American species of the section, *T. maculata*, in having pubescent leaves (discussion under *T. maculata*).

Additional specimens examined. PANAMA. LOS SANTOS: Monagre Beach, *Dwyer 4182* (MO (2)). PANAMÁ: Coronado Beach, 6 mi. E of San Carlos, *Croat 14261* (MO); near Playa Río Mar, 10–100 ft., *Duke 11761* (MO).

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